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THE STUDY OF BIRDS

AN INTRODUCTION TO ORNITHOLOGY

By E. M. NICHOLSON

Author of Birds in England How Birds Live etc



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THE STUDY OF BIRDS

CHAPTER I

INTRODUCTORY

A BIRD is known by its feathers, not only proverbially, but in scientific definition. Certainly it has other obvious characters—of flight, of going on two feet, and of laying eggs instead of bringing forth the young alive—but considered as points of distinction these are of less essential importance, since there are mammals which do each of these things, and, on the other hand, birds which cannot fly. In the scale of life it comes next after the mammal, but its relationship to the reptile is much more marked. In fact, both these undoubtedly spring from a common stock, and the most primitive of fossil birds might almost be mistaken for a reptile. A bird has the hottest blood (up to 112° Fahrenheit) and therefore the swiftest nervous reactions of any vertebrate. Its brain is not remarkable, but it possesses a set of fine instincts sufficient for the demands which life commonly makes on it, and it combines extreme vitality with most enviable powers of endurance. At its best it is the most free of all animals except man, enjoying long life and perfect health, the power of freely changing its environment, and faculties which are a source of constant pleasure, like flight or elaborate song. Yet it is

essentially a slave, being incapable of reflection except in the most primitive sense and entirely at the mercy of a series of delicate yet not especially subtle trains of behaviour, to which the circumstances of the outer world are perpetually acting as a stimulus or "trigger." A human being who possessed the mentality of a bird would be considered irresponsible, unintelligent, but gifted with inexhaustible intuitions, quite lacking in character but ready and alert, unimaginative, and entirely without any morals.

In size a bird may range from a creature no bigger than a beetle to something considerably taller than a man; its tail may be practically absent or prolonged to a far greater length than the body it belongs to; its wings may be developed to the extent that it is hardly able to alight with comfort, or so atrophied that it cannot fly; it is by nature prone to the most fantastic extravagances of colour, of ornament, of voice, of behaviour, or of specialised adaptation.

It is clear, then, that the study of birds, which we call ornithology, is curiously full of pitfalls. There is so much temptation to be diverted into the mere cataloguing of plumages, the chronicling of wanderers far outside their range, into idle theorising about migration, collecting pretty pictures or beautiful eggs, or regarding with a gush of sentiment these beings so conspicuously free from the evils to which ourselves are conspicuously exposed. Yet these activities, although birds are their subject or their victim, have little else in common with ornithology proper. Some of them had once a real value which they have obstinately outlived; others never had any value except of a negative sort, nor ever will. Orni-

thology, as it is to be considered in these pages, must be taken as the dispassionate concerted effort of a few men (separated by wide tracts of time and space) to attain, through constructive observation, to a more profound understanding of birds. We will, therefore, best fulfil our purpose, not by reviewing the various orders and families of birds, their distinguishing marks, their peculiar habits, and the number or kind of eggs they lay, but by outlining the principal methods by which ornithology is at present proceeding, and the problems which it is solving, or hopes to solve in the future.

CHAPTER II

HISTORY OF ORNITHOLOGY

ALTHOUGH the ancient Egyptians were expert enough to leave us a remarkable likeness of the red-breasted goose, and there are some well-known references to birds in the Old Testament, the science of ornithology must be taken to begin with Aristotle. He encountered the subject in the course of his monumental survey of human knowledge, and was never able to devote himself to it with much detail, but, like everything else he touched, ornithology was permanently enriched by his fruitful and penetrating mind. As the dominant influence in medieval learning he ought to have been able to stimulate some of the intellectuals between the thirteenth and fifteenth centuries into paying some attention to the study of birds, but the Middle Ages were too biassed in the other direction to be attracted by any sort of science. It was only when they gave way to the Renaissance, and when their teacher himself shared the fate of Don Quixote, that disciples of Aristotle began to appear to carry on this particular branch of his researches. It was doubly unfortunate for his reputation as a naturalist that after such long neglect he should have been resurrected chiefly in order to pour scorn upon the fables which he occasionally allowed to deceive him. A philosopher, with almost a blank sheet to start with, was not likely to be unimpeachably

accurate on questions of fact, but there has never been an ornithologist who had such ample excuse for his errors, and the congenial task of pointing out that cuckoos do not turn into hawks every winter, nor geese hatch out of barnacles, may easily lead us to overlook how fundamentally his observations are true. His data were few and faulty, but he had a fine and discerning mind reinforced by a wide knowledge of men and things, which enabled him better than almost any of his successors to realise the true function of natural history among the sciences. He clearly understood that anything like the pursuit of birds for birds' sake, whether as a collector of skins or eggs, pictures or memories and impressions, could never be the worthy object of a science, which, if it is to fulfil itself, must work by the means at its disposal towards a solution of the scheme of things. Ornithology, that is to say, must not be content merely to set before itself a complete understanding of birds; it must aim at the understanding of life itself so far as birds can throw any light upon it. Acting on this conviction, Aristotle not only brought to bear on natural history his great extraneous learning, but used his knowledge of Nature, on the other hand, to illuminate his view of human institutions. One particular passage from the *Politics* is worth quoting here, since it forms incidentally a much better general statement of the territory theory, so important in modern ornithology, than anything which I could find elsewhere, or hope to compose myself:

“Again there are many sorts of food; and therefore there are many kinds of lives both of animals and men: they must all have food, and the differences in

their food have made the differences in their ways of life. For of beasts some are gregarious, others are solitary; they live in the way which is best adapted to sustain them, accordingly as they are carnivorous or herbivorous or omnivorous; and their habits are determined for them by nature in such a manner that they may obtain with greater facility the food of their choice."

Only during the present century have zoologists begun properly to grasp that economic basis of social organisation and distribution among animals which is asserted here in words written over two thousand years ago.

When modern ornithology awakened, as it first did with the works of men like Gesner, Dean Turner of Wells, Belon, and Dr. Caius in the sixteenth century, it took on a strong and almost fatal bias towards rarities and freaks. The generations whose poets were attracted towards "... the Anthropophagi, and men whose heads do grow beneath their shoulders" produced as a matter of course scientists obsessed with insignificant and rather disgusting abnormalities, like kittens with two heads, monstrous births of all kinds, enormous gall-stones, or horns of supposed human growth. The whole tendency was to despise and practically disregard whatever was common and to exalt the extraordinary or the rare, 'specimens' of which began to be hoarded in dusty and verminous museums, where there was little labelling and no arrangement at all. This futile tradition, although long ago discredited, continues to stifle the progress of ornithology to this day. It shows itself especially in the abysmal condition of most of the

collections of "stuffed birds," at any rate in Europe, and in the unreasoning worship of rarity common to those who collect and those who simply observe. The cult of varieties and freaks is slowly losing ground, although they are still considered better worth recording than facts for the want of which ornithology is at many points held up. We can only understand the present position when we consider that, in England at least, it would be more feasible to take a census of pied blackbirds or of white sparrows than of any common species, the statistics of which would have a certain scientific value.

We may say without serious injustice that the sixteenth and seventeenth centuries, with a great part of the eighteenth, were consumed, so far as ornithology was concerned, in the enumeration of species and the compilation of facts about their plumage, reproduction, and their more striking habits. It was mostly hack work, involving little genuine research and wholesale borrowings from earlier writers, and there is no reason to be surprised that no first-rate figure appears in it. In so brief a sketch as this it is only necessary to name the Englishmen, Francis Willughby (1635-1672) and John Ray (1627-1705), who laid the foundations of scientific classification, and Linnæus the Swede (1707-1778) who reduced all the species of plants and animals—birds, of course, included—to an orderly system of Nature, in which he allotted every known species to its genus, every genus to its order, and every order to its class. Except for the separation of sub-species, of which any species may possess a large number or only one, and the discrimination of the family, his work is still the basis

of classification, upon which subject more must be said later.

During the lifetime of Linnæus natural history became popular. Before the *Lyrical Ballads* had lent Nature a romantic prestige, even during the most formal and classical epoch, when Versailles set the tone of European civilisation, a tendency towards nature-worship began to appear. Under such influences as Thomson's *Seasons* in England and Buffon's glowing prose in France to know something about Nature became definitely a fashionable accomplishment. Although the Nature thus embraced with as much enthusiasm as the eighteenth century would permit itself to show was not quite Nature as we know her, but something much more orderly, in harmony with reason and a broad-minded theology, yet this popular interest was bound to have most tremendous effects. It meant that natural history could no longer be the special preserve of a rather dull and pedantic set of men, but must accustom itself at least to being interpreted in terms of ordinary lay experience. The condition was for the first time imposed that natural history must be made interesting, and it is significant to find Buffon, the most typical naturalist of the period, asserting most positively that only those books would live which were the best written. Now, when it becomes a question of popular appeal, birds have an easy superiority over any other branch of natural history; it therefore happened that ornithology, which had hitherto had to depend largely on an occasional fillip from some versatile botanist or doctor, suddenly passed into the hands of a large corps of enthusiasts, some of whom

cared for very little else. Botany and entomology, which had both had a better start, lost something of their lead; mammals got rather lost between the game-hunter and the museum zoologist, fishes and reptiles suffered from a neglect which to some extent still persists. Birds, a comparatively small and limited class, rose rapidly to a popularity which they have never had to yield.

The period while this change was taking place is spanned by the lives of two men whose work had a lasting influence upon ornithology. Gilbert White (1720-1793), beginning from a quite conventional passion for gardening, turned, under the influence of some of the leading naturalists of his day, to a general observation of Nature, and especially of birds. He was not particularly interested in the systematic work or the oddities which had absorbed his predecessors, and he set himself to find out something about the ordinary life of the ordinary animals of his parish. Half-unconsciously he became the leading figure in a revolution of method and outlook, for no one who read his observations, taken directly from Nature with a penetration and sense of proportion which had never before been concentrated on the subject so long, could continue to tolerate the arid repetitions of the standard natural history at that time. His *Natural History of Selborne*, limited as it was to a single parish, was at once translated into German, and has run through endless editions in Great Britain and America from its publication in 1789 until the present day. It is the outstanding classic of natural history, to be read with increasing pleasure over and over again, and its influence on succeeding ornithologists has been tre-

mendous. One of its first and most enthusiastic readers was Colonel George Montagu, who applied White's principles with conspicuous success in his *Ornithological Dictionary*, the basis of all the standard works on British birds which have been written since 1802.

Unfortunately, firearms developed more rapidly than ornithology. Through most of the nineteenth century slaughter of specimens and accumulation of egg-shells proceeded on a colossal scale. Of course a certain number of specimens were needed in order to distinguish the various species and to elucidate their changes of plumage and their relationship to one another. But this wholesale killing and looting was not only far in excess of scientific requirements at the time, but had rarely the justification of being done in any scientific spirit or on scientific lines. Every specimen which is to be of any serious value, ought to have attached to it the minimum of data as to where it was procured, on what date and by whom, with the colour of the soft parts recorded at the moment, and the sex as determined by dissection. In few cases was this duty adequately performed, and in many there was no attempt to perform it. Masses of specimens were wasted in every part of the world, and many which were brought home to English museums from abroad lay stored without any arrangement, and identification, or any efficient preservative, until they finally had to be thrown away. There are even now few British museums, large or small, which do not conceal relics of this senseless and unscientific slaughter, seen by their custodians only at an occasional spring-cleaning and by the public

never. The stuffed birds which ornamented the houses of persons of ornithological tastes and a great many hotels are equally an indication of the nineteenth-century spirit. But this period, however wastefully, did succeed in sorting out the birds of the world in a comparatively thorough manner, and towards its end the haphazard collection of material about habits—especially, of course, peculiar ones—grew into a fine and intensive study of life-history. In England the outstanding figure of this school was W. H. Hudson, followed more lately by Edmund Selous (who brought it to an astonishing degree of intensity) and by Professor Julian Huxley, who has restricted himself mainly to courtship and display.

The opportunity for such purely individual observation was, however, nearly lost through the long delay in taking it up, and when it at last showed signs of flourishing most of its potential recruits were absorbed by newer activities. Bird photography, which promised to combine the obtaining of valuable pictures with a rich harvest of observations gained during long periods of intimate contact with breeding birds, absorbed the energies and enthusiasm of a large number. But to these the photography has usually proved of more importance than the bird; they are with few exceptions photographers first and ornithologists afterwards, and in comparison with their opportunities their contributions to the sum of knowledge have been disappointing. Bird-marking and the bird census, which also made their effective appearance about a generation ago, have become such important instruments of research that they must form the subject of special chapters. The territory

theory, foreshadowed as we have seen by Aristotle and later by Gilbert White and others—even Oliver Goldsmith was aware of the territorial holdings of the robin—began in the twentieth century to be properly worked out, and since its essential problems were exposed by H. Eliot Howard in his *British Warblers* (1907-1914) the fundamental importance of the subject has been more nearly realised, and a certain, although quite inadequate, amount of field observation has been done on it. Bird protection, which was brought to the front by the unlimited slaughter during the nineteenth century, and the need for preserving many species from the extinction then rapidly overtaking them, has also to be dealt with elsewhere. By 1900 we have reached the point where ornithology ceases to be a history, and becomes an account of the lines of current work.

CHAPTER III

CLASSIFICATION AND COLLECTING

It needs no expert knowledge to detect that a sparrow is more closely related to a starling than a starling to a swan. The most elementary study of birds is sufficient to bring out the fact that there are many individuals, identical in heredity and often in plumage, interbreeding regularly with one another and with none else, and such a group is recognised as a *Species*, distinguishable from other species by superficial characters of form and habit, sometimes very slight, sometimes extremely conspicuous. Nor do we have to go very far before realising that the species themselves fall into groups, and we divide these groups of species into three degrees of consanguinity; first, the *Genus*, confined to very close relations having all their fundamental characters in common, then the *Family*, which may include many genera, and finally the *Order*, which unites all families conforming to the same general specification. The sequence in which these Orders should be taken, and of the various families within them, is still a matter of dispute, British naturalists usually beginning with the *Passeres* and finishing up with game-birds, while Americans do almost the opposite. But there is general agreement on the principles according to which classification should proceed, and the position of any given species with regard to its relationships is not very difficult to establish.

But the world talks an infinite number of languages, and scientists come from many races; in the absence of any central international clearing-house the difficulty has always been to prevent overlapping and duplication through workers in different countries remaining in ignorance of what has been done abroad. The retention of Latin descriptions, and their publication in recognised specialist journals, has done much to bring the scattered efforts of ornithology into line, but the ideal that any given species should be known universally by a single scientific name, to be used on all labels and references in whatever language they are written, is still by no means realised. Difficulties are bound to arise when the same name is given by two men independently to different birds, or different names to the same bird, and the obvious solution of rigidly adopting the first to be published—the rule of strict priority—is not in practice as efficient as it might be. Partly, it is not always easy to establish, in the case of old and obscure works, which actually appeared first; and partly, it has encouraged the growth of a small school of pedantic and antiquarian ornithologists who spend their time unearthing forgotten sale catalogues and other limbo of the eighteenth and early nineteenth centuries, in order to have the pleasure of upsetting names used unquestioningly by three or four generations of ornithologists.

Probably the most conspicuous example of the inconvenience which may result is that of the common European song-thrush or throstle. For a century and a half this bird was universally known as *Turdus musicus* (Linnæus) until it was shown that the bird intended by Linnæus in his description was actually

the redwing, which had always been called *Turdus iliacus*. In the absence of any spirit of reasonableness, or of any authoritative body whose decisions could be satisfactorily enforced, it was impossible to do anything but bow to the established rule—transfer the name *musicus* to the redwing, in spite of the great confusion involved, and rechristen the song-thrush *T. philomelos*, that being the next senior name. Only a few years later it was claimed that the designation *T. ericetorum*, which had just been unearthed by a too persistent investigation, was prior to *philomelos* and ought to supersede it, but the worm of ornithology turned, as it should have done much earlier, and the pure logic of priority failed to make any impression on common sense reinforced by weariness of the flesh. The majority is by now so tired of the raking up of names which have never been adopted that further enterprise of this sort is likely to be discouraged.

Another fruitful source of dissension has been the question of sub-species, or geographical races. It became apparent, almost as soon as ornithology got down to detail, that there were forms so nearly alike and so prone to interbreeding that they could hardly be called good species, and yet distinguished by sufficiently clear characters (often including a difference of geographical range), to deserve some recognition of their existence. For long the die-hards turned a blind eye upon such creatures, granting specific rank to the most inconveniently obvious races, and until the present century the war between the "lumpers" and the "splitters" was not decided in favour of the latter. It is now conceded that any species may be divisible

into two or more sub-species distinguished by a different range of measurements, or differences of plumage, perhaps only in one sex or at one season, or differences of geographical range, or all three characters, the last being the most important, because the others are more or less conditioned by it. As an instance of the type of nomenclature now in force, the raven belongs to the Class *Aves* (birds), the Order *Passeres* (perching birds), the Family *Corvidæ* (crows), and the Genus *Corvus* (true crows). The full scientific name of the typical European sub-species is *Corvus corax corax* (Linnæus), while the American is *Corvus corax principalis*, being a distinct geographical race. The sand-martin, known in America as the bank-swallow, is in the curious but not unusual position of having for its typical race the same generic, specific, and sub-specific name, *Riparia riparia riparia* (Linnæus).

It is easy when disputes over nomenclature arise, as they so frequently do, for the non-systematic ornithologist to cry a plague on both the houses of the protagonists and to doubt whether the convenience of a universal common standard (existing rather in theory than in actual practice) cannot be too dearly bought. Certainly those who are most obsessed with correct nomenclature and the separation of geographic races are the worst enemies of the causes they uphold; by constantly exaggerating the importance of really trivial points they alienate workers with a better sense of proportion, and if "skin-sorters" is merely one of the more polite of their common designations they have only themselves to thank for it. Yet it needs very little reflection to see that, mechanical and unfruitful as systematy inevitably is, ornithologists

ought to be very grateful to those who have plodded through it. It bears the same relation to the subject as a whole that an index bears to a voluminous book; and if the index-makers have often proved quarrelsome and small-minded, the positive value of their labours is not very much the worse for it. As to that metaphor we must confess that if those responsible for the text had come as near to the completion of their task as those who have been indexing the headings, ornithology would not be in nearly such a backward state as it now is. Since it is necessary that systematy should be worked out, it is equally necessary for collecting to be done, seeing that he who wills the end wills the means. The identification of species, the separation of sub-species, and the elucidation of changes of plumage can only be accomplished when the museum specialists who follow these lines of research have at their disposal a sufficient series of skins, accompanied by authentic data, to form a basis for unexceptionable conclusions.

When we hear an outcry against the collector as an exterminator of rare birds, and find some ornithologists, including the present writer, even arguing in favour of the suppression of private collections, we must not forget that there are valuable branches of ornithology to which collecting is essential. It is not collecting that has proved useless and mischievous, but the average private collector. Relying on the cloak of a scientific mission to protect him, he has during the last hundred and fifty years enjoyed a very happy time pursuing the rarest birds in order to preserve their stuffed corpses in glass cases. He has bribed all sorts of accomplices to persecute them in their few haunts,

defined protection orders, neglected to record the minimum amount of data indispensable for scientific purposes, and followed a secretive individualistic line, contributing little to the common stock of ornithology. The great majority of private collectors have never been scientists following a definite line of research; they have been shooters with an itch for acquiring specimens of rare species, or freakish examples of common ones. Oology, the science of birds' eggs, has proved even more futile. There were always some scientists in the background, to give colour to the exploitation practised in their name by the ordinary private collector of skins, but the subject of eggs, except from an embryological standpoint, has never been scientifically investigated. The result is that after generations of wholesale and senseless accumulation of pricked egg-shells, the simplest facts about these curiously variable and characteristically avian productions remain completely unexplained.

The rules which ought to be followed in the collection of birds and eggs are sufficiently clear. A species more or less rare should never be made the subject of destructive inquiry in connection with any point which might equally well be investigated in a common one. It should be interfered with on no pretext whatever if there is any reason to suppose that the toll may endanger to the slightest degree its existence, even locally. No bird should be shot in circumstances when it is likely to be irretrievable, or too badly damaged for preservation, or where there is no possibility of its being decently skinned. Natives, where any are employed, should never be encouraged to shoot birds indiscriminately; they should be forbidden to continue

to kill birds of which enough specimens have already been secured, or to bring in anything because they think it ornamental. The collector who fosters the belief that there is any intrinsic value in birds or their eggs, and persuades the natives to take up their persecution, whether in Uganda or the Hebrides, has a heavy responsibility. It is the duty of the collector to extract the utmost scientific significance from every specimen he obtains. That is to say, he ought in ordinary circumstances not only to ensure that the specimen is well skinned and clearly labelled, with full data regarding locality, time, and agent responsible for it, colour of soft parts—bill, feet, irides, and orbital ring or wattles if any—at the hour of death, and sex reliably ascertained by dissection; but he should also record the weight, preserve in a distinct and identifiable container the contents of the stomach and crop (unless they can be satisfactorily enumerated on the spot), and look for parasites or any signs of disease. If any serious attempt in this direction had been made by former collectors, one-hundredth of the birds collected would have added ten times as much to our knowledge. As for birds' eggs, except where they happen not to have been reliably recorded, or where the existing series of authentic specimens is too small for an average measurement to be arrived at, it is exceedingly doubtful whether their collection, except by qualified biologists, for one or two highly specified branches of research, has any scientific value at all.

Unlike the individual observer, but like the bird marker and census-taker, the collector does not usually operate on his own. He may have associates in the field, especially on foreign expeditions, and in any

case, if he is working seriously and not merely to gratify a selfish and destructive hobby, he must frequently have recourse to a museum—so frequently, in fact, that it might almost be said that every honest collector is the agent of a museum, either paid or honorary. There are, of course, a great many institutions labelled “museum” scattered over almost every civilised country, and most of these have some sort of a collection of stuffed birds, because stuffed birds are among the exhibits with the most universal popular appeal. But few of these institutions are from an ornithological standpoint to be taken seriously. It is useful to bear in mind, so long as one does not push it too far, that the scientific value of a collection of birds can be approximately gauged by their general state of preservation and by the proportion of skins to stuffed specimens. Broadly speaking, the specimen of scientific importance is a skin; the stuffed bird is not so much a scientific exhibit as an object for popular display. It serves to amuse the public and give some rough idea of what the species looks like in life; the most ambitious galleries also aim at reproducing its natural surroundings, together with the nest and eggs or young, and perhaps the characteristic diet so as to present a memorable picture. But such exhibits are not of much scientific value, and are, in fact, often inaccurate in points of detail; thus the fulmar petrel appears in almost every museum stuffed in a standing posture, which the living bird is quite incapable of adopting owing to the weakness of its legs; and the discovery that the cuckoo lays its egg directly into the nest seems so far to have escaped the attention of many curators, whose exhibits are based

on the contrary belief. There is no doubt, in fact, that the display of birds in museums, at any rate in Western Europe, leaves very much to be desired.

The museum which realised its true functions, so far as its bird collections were concerned, would give prominence to special exhibits illustrating in the most graphic form aspects of bird economics, protection, migration, adaptation, and the progress of such lines of research as bird-marking and the census. To a very limited extent this is gradually being done; but the special exhibit ought to be promoted from the status of a mere side-show to the main activity of the bird galleries, which should make it their business to keep the public vividly in touch with the efforts and progress of ornithology. They should aim at providing for identification purposes a faithful representation of every species known to have occurred or likely to occur in the surrounding country, not so much through the expensive medium of dusty and faded stuffed effigies as through a gallery of all the best figures, particularly coloured ones, which could be taken from available standard books and suitably framed on stands—a scheme which has been carried out with notable success at Haslemere Educational Museum, and perhaps elsewhere. Yet as we have already found, the exhibition galleries, enormously as they might be improved, are not the most important part of a great museum. It is not they but the study collections that really settle to which grade a museum belongs. In the British Isles there are probably only two which are by this standard of first-rate importance; one is the British Museum (Natural History) at South Kensington, and the other is almost unique in being a private

collection, the Rothschild Zoological Museum at Tring. Unique, that is to say, in being a private collection run on scientifically productive lines and forming a definite unit among the limited ornithological resources of Europe. Of course, Dublin and several provincial museums in the United Kingdom possess study collections of not inconsiderable extent, but with very few exceptions they are too understaffed to be able to do anything to further research. Apart from the British Isles, probably the most important museums, at least as centres of research, are to be found in the United States, Germany, and Denmark, but most of the so-called Nordic countries are more or less active in this direction. France and the Latin and Slavic nations (except Hungary) are considerably less so, and the Orient quite stagnant, with the conspicuous exception of Japan.

It is to the study collections that almost all specimens of real scientific value sooner or later find their way. Such institutions cannot, of course, compete with rich men of perverted tastes for the costly surviving specimens of the great auk and its eggs, but the mania for collecting is not strikingly hereditary. If the founder of a collection does not bequeath it to the public, his heirs (after disposing of any saleable items) are generally only too thankful to palm off the white elephant on any museum willing to accept it. Under this system decently labelled collections of any special interest usually go to the national museums, while the general ruck remains for the provincial, which, in their present neglected and understaffed condition, rarely deserve anything much better than the rubbish they usually get.

CHAPTER IV

HOW TO OBSERVE

ONE cannot observe without a theory, and what seems the simplest of ornithological tasks—to go out of doors and look out for something worth recording—is in reality one of the hardest. Many people can collect birds, skin them, photograph them, draw them, mark them, count them, or describe their plumages with considerable efficiency, but real observers are very few, and there never has been an observer yet who was not very limited and obtuse compared with what he might have been. It is a mistake to imagine that complete impartiality and freedom from preconceived ideas is the qualification for a perfect observer. The cow is an animal with a remarkably open mind, yet it has never been found to reach a high degree of civilisation. Most bad observers probably approach the subject with much more open minds than most good ones. The reason is not that impartiality is an evil, but that in itself it is a complete bar to observation. To speculate on the unknown involves applying to it the inevitable bias of an ungodlike mind. Yet one must have thought about a subject, or at any rate about an allied one, in order to be able to notice anything at all detailed relating to it. Every day a great many ordinary people without any interest in birds are present when things take place which some ornithologists would give a great deal to watch, but these people not only

fail to record what they see, they fail even to see it, because they are not looking out for it and there is no place in their minds for it to fit in. A naturalist whose friends attempt to learn from him the songs of common English birds is shocked at first to discover quite intelligent people of good hearing repeatedly failing to distinguish accurately between the black-bird's song and the throstle's, or the chaffinch's and the robin's, which are to him as far apart as a dog's bark and a goat's bleat. The reason is that they possess at first no standard in their minds which will serve; it is easy to pick up quite rapidly the difference between two very similar strains when one is familiar with many, but the first half-dozen, however distinct, take a long time.

It is necessary, then, for the observer to be trained, and by *trained* something more must be understood than mere practice in watching birds without scaring them away. There are many people—the type is especially common among gamekeepers, shooters, and sanctuary-wardens—who have been watching birds all their lives and are nevertheless thoroughly unreliable on any but the most obvious questions of fact, not because they are untruthful, but because their minds have never undergone the discipline of testing each observation till it is proved to be quite sound and watertight, and of always being ready to meet expert criticism. The very conflicting detailed accounts which are often given in perfect good faith at an inquest into an accident or a crime are a familiar instance of the same shortcoming. And when we remember that every observer, whenever he investigates anything new, has to act first as a detective and later as a coroner or judge, the subjects

of his inquiry being incapable of giving any account of themselves and often unwilling even to be watched, it is not hard to realise why competent observers are so rare. They need not only keen faculties (or at least one keen faculty, either hearing or sight), training, and much patience, but some qualities of mind rarely found together—imagination, ability to know exactly when a thing is proved, a command of language, and some aptness in description, precision over facts, and something like fertility in theory, to mention only some of them.

It seems inevitable that first-rate all-round observers should always be too rare, but there is no doubt at all that the general level of observation, and the usefulness of the ordinary observer might be enormously improved. A multiplicity of lines of research held up for lack of the most simple data (which no one happens to have got), and, on the other hand, thousands of potential observers wasting their time on the futile recording of early migrants, albino sparrows, or chance vagrants on reservoirs and sewage farms—that is the unhappy spectacle which ornithology at this moment presents. The same is true not only of England, but *mutatis mutandis* of almost all parts of the world where anything is being done at all. Indeed, judging by the pioneer investigations along such lines as bird-marking and the territory theory, England, with the Teutonic countries of North-Western Europe, is the least backward, although in the important matter of a bird census, the United States has always taken the lead in large-scale operations. It is not, however, desirable to go into any detail here, the point to be made being simply

there is no truth whatever in the easy and fatal belief that ornithology is almost worked out. That belief has persisted since a long time ago; it is amusing to find an author of Yarrell's period (1784-1856), in what we should call the Dark Ages of ornithology, apologising for his work on the same ground, and merely venturing to hope that, everything of importance being already known, he had presented the subject in rather a better arrangement than his forerunners.

Ornithology, as a matter of fact, has hardly begun; in this little book we are sketching the outlines of an incipient science rather than expounding the principles of an established one. The delusion that nothing remains to be discovered is the inevitable result of the false and perverted view of ornithology which was long current, and lingers even now. What was venerated yesterday as a standard work forming the Alpha and Omega of the study of birds will be regarded to-morrow as a mere collector's handbook, giving, without remarkable accuracy, the descriptions of species with their nests and eggs, the crudest account of their distribution, and practically nothing besides.

The first thing, then, to be borne in mind is that there is at the present time probably no part of the earth's surface, land or water, where there is not fruitful observation to be done. High altitudes, great cities, deserts, and ice-fields, like all highly specialised environments, are liable to a monotonous and perhaps very limited avifauna, but even these present to the observer with vision immense opportunities for constructive study. In towns, even the largest, which are generally considered hopeless by the average ornitho-

logist, there are more significant adaptations and more developments to be observed in rapid progress than in most of the famous show-places to which he is always yearning to dash off. Similarly, there is no bird in the world, not even the sparrow, about which a good deal of the first importance does not still await investigation, whenever an observer appears with the patience and the imagination to get to grips with it. In reality the field is so infinite that the difficulty is to avoid dissipating one's energies, and this applies equally to each individual worker and to the science as a whole, which is at present attacking the most intricate problems of migration, economics, and so on, with resources hardly sufficient to deal adequately with any one of them by itself. It is desirable, therefore, to take one line, or at any rate two or three lines and keep to them, rather than to act as an opportunist pursuing for a time whatever happens to turn up.

If you are at the stage when you can discern nothing worthy of note except a hawk striking down an owl, or a nest in a tin can, or a crow with a malformed bill, it will no doubt seem at first that this is a counsel of perfection condemning you to a very small return for your labour, but in practice it is not so. As you get deeper and deeper into your subject the remarkable events multiply, because all sorts of things dismissed as insignificant before, and many which were never noticed, take on a vital meaning. Thus the average observer will perhaps note the dates on which various species begin and cease their song, and the character of the song, and very little else, whereas anyone engaged in tracing the connection be-

tween song and territory will discover, if his hearing is good, a whole new world of primitive whispered sub-songs betraying the most unexpected likenesses. He will look out eagerly for any case of a bird singing its true song while still belonging to a winter flock, or for a hen bird uttering anything like song or sub-song, and for courtship accompanying song or preceding it. He will notice with surprise and almost incredulity how large a part is played by song in making the smaller and duller birds conspicuous at that stage of the breeding season when they have to be so in order to warn off rivals and to attract a mate, and how the song is often accompanied by a new habit of lofty perching, or of dancing in the air, which serves to reinforce this effect. In fact, once the observer is launched on the right track, every song he hears, even of the most abundant species, will become positively or negatively a valuable clue, and the most casual allusions to a song in books will become invested with a rich significance of which the writer was probably entirely unaware. The most trivial incidents, like two cocks of a territorial species perched on the same stone, become to the trained field-ornithologist data which may help to confirm or to modify a fundamental theory of bird life. It is true that the egg-collector shares with the true observer this absorbing interest in the apparently insignificant, but there is no comparison between them, for while the oologist gloats over eggs for eggs' sake, the observer is only interested in his facts precisely in proportion to the light they throw upon bird life—it is not the facts, but their aid in solving ornithological problems which form the attraction.

It is difficult at this stage to lay down any very satisfactory rules about observation, but certain principles are plain. The ornithologist should choose his field largely, of course, according to his own inclination (for he is likely to do best what most appeals to him), but also with regard to the resources of the area in which he lives, unless he has unusual opportunities for travel. Thus there are obviously some districts particularly suited for the study of bird communities, others for migration, others for the effects of sweeping changes in environment caused by building, droughts, floods, storms, agriculture, or drainage. It would not only be difficult to make any useful study of, say, communities, in an area where hardly any important social forms existed, but it would be waste of opportunity to follow in country specially favourable to one line of research a different line which could be done better elsewhere. On the whole, districts as compared with one another are not "good" or "bad" for birds, as most people believe, but merely different; the popular idea is due to the fact that everything is eternally being considered from one narrow angle of the pursuit of rarity. A "good" district is accordingly one which is attractive for that often harmless, but rarely useful, line of observation, and a "bad" district one which is not. The assumption only needs to be analysed in this way to show how ridiculous it is, and it brings about the paradoxical result that facts about rare birds are recorded in such disproportionate detail that often more is known about them, not only relatively, but absolutely, than about the despised creatures which haunt our own gardens and form the preponderant influence in

our wild life. It is probably no coincidence that almost all the observation of most permanent value, taking the case of England, has been done not in the "good" areas, along the coast and elsewhere, but by inland observers in remarkably "bad" districts for birds. Thus, Gilbert White worked on the edge of the Hampshire chalk mass, Jenner in Gloucestershire, Eliot Howard and Chance in Worcestershire; W. H. Hudson was tied down in London, while the Oxford Ornithological Society has been stimulated towards some pioneer efforts in corporate field work by the ordinariness of the South Midlands.

It is desirable, then, for the field ornithologist to pursue some fairly definite idea, selected partly according to his desires, partly according to the opportunities of the country in which he finds himself. He will rarely, however, be able to foresee at the moment of first being attracted to it how far it is going to lead him. To suggest schemes of observation hardly falls within the scope of this work, and the present writer has already attempted something of the sort in a previous publication (*How Birds Live*, 2nd edition, London, 1929). It seems, nevertheless, desirable to sketch very briefly a few of the problems most urgently in need of field inquiry which lie within the capacity of an ordinary observer without any special scientific qualification.

There are at present hardly any satisfactory data on the subject of non-breeding birds. It is well known that many of the larger forms do not assume mature plumage and begin to breed until the end of their second year, and even very much later, so that, however long they live, the non-breeding stock is bound to

form a large, and possibly the larger, part of the whole population at any given moment. The same thing may happen in the case of smaller species. For example, Mr. C. B. Moffat has shown reason to suspect it in the case of the European house-martin. But in any case there are always members of almost every species which, from one cause or another, do not breed, and at the vital period most ornithologists have usually been too obsessed with the hunt for nests to pay any attention to the question. We still do not know, either generally or locally, whether the army of non-breeding birds is permanent or whether it tends to disappear in favourable seasons and to increase in bad ones, nor whether there is a preponderance of one sex, and how far it may be responsible. It is a problem demanding patience and close observation at the right season rather than any special knowledge, since it might to a great extent be solved by a sufficient series of answers to such simple questions as these: Do all the local birds which stay through the breeding season attempt to breed? Assuming they do not, to which species and sex do any non-breeding birds observed belong? How do they live while the others are breeding, and what is their attitude towards the parent birds near them and to one another? Does the strength or composition of this non-breeding population vary at all from year to year? Has failure to breed any apparent connection with the status of the species concerned—resident or migrant, rare or abundant, territorial or communistic?

Or take competition. In almost every country there are instances of species either closely related or of similar range and diet, which seem likely to be rivals

for food-supply or nesting-sites, or both. Even where no visible hostility exists, one may gradually be replacing another through sheer economic pressure. Or one may have the advantage where the soil and vegetation are of a certain character, and at the point where it changes the advantage may pass to a rival. There are numerous suggestions that this sort of thing may occur, and may have important effects on distribution; it is impossible to say more because in scarcely any instance has the slightest attempt been made to work them out.

Again, there are certainly many cases of commensalism which have still to be detected before the subject can be considered anything but obscure. Commensalism implies species living together and gaining something by it for one party or perhaps both, without developing any sort of parasitic relation. Thus, while acting as ornithologist to the Oxford University Greenland Expedition of 1928, I found that along the coast of the fiord, where the arctic skuas (or jaegers) were quartered, the red-necked (or northern) phalarope was only to be found breeding in those swampy areas where a pair of ptarmigan had established themselves. The reason apparently is that any phalarope attempting to breed upon a skua territory would be doomed to destruction unless it could rely on the protection of the ptarmigan, which is the only local bird harmless in itself and yet sufficiently bold and vigilant always to repulse an approaching skua. In doing this, of course, the ptarmigan is concerned simply about the safety of his own mate and brood, without any regard for the helpless phalarope, but the phalarope, so long as it nests always within a ptarmigan territory, is able

to enjoy an immunity which it could never secure itself. There must be a good deal of commensalism among mixed flocks of different species, although very little has so far been detected owing to the meagre attention the point has hitherto received.

Again, many birds outside the breeding season resort to roosts a long way from their foraging areas. This is true, for instance, of many aquatic birds, and of such a widely distributed passerine species as the starling. Although a certain number of roosts have been observed, much more will have to be done in the way of tracing out fly-lines and mapping them locally in detail, before it is possible to say with any confidence what the factors are which govern the choice of roosting-places, from what distances their inhabitants are drawn, and what advantages a single great central dormitory has over the habit of roosting dispersed near the feeding grounds. Similarly, the foraging range of the communities which sometimes people a bird-rock, a marsh, a sandy spit, an islet, a lagoon, or a group of trees, needs to be carefully observed, in order to ascertain the real density of population over the whole area from which food supplies are being obtained, the powers of flight of the species concerned, and the extent of its contacts with other forms of life.

Fertility among different species varies most strikingly in different parts of their range, both as regards the number of broods and the size of clutch in each, and further, of course, the proportion of young reared. It is very necessary that a great many more data should be recorded on such points, as well as the proportion of eggs laid which are destroyed before and after hatching—that is to say, mortality in the nest—

and the causes of disaster, whether through human, animal, or climatic agency. This is chiefly a matter of statistics, and so overlaps with the bird census, with which, in fact, it may very advantageously be combined. To count all the birds on a small area of, say, twenty or forty acres and devote the breeding season to tracking down all their nests, recording how many eggs are laid and how many young reared, with the mortality details above mentioned, is at the moment one of the most valuable services which it is in the power of the ordinary observer to perform. On the other hand, a set of such details for all the nests which happen to be met with, not attempting completeness for any special area, is also of value provided one season is kept separate from another. The incubation and fledging periods of many of the commonest birds, even in England, are still very imperfectly known. Although it demands absolute accuracy and considerable care to establish the exact period without disturbing the subjects of inquiry, this is also an opportunity open to any student of birds without special qualifications. In taking up such a research it is desirable to record in as many separate instances as possible the date of laying of each egg, or indispensably that of the last egg, the date of hatching for the first and last chick, and the date of fledging—facts which must not be affected by any abnormal outside agency, or by the carelessness of the observer, if they are to be of any value.

Gregariousness, where it occurs freely, is always an interesting subject for study. The manner in which flocks come together, whether by the fusion of family parties after the breeding season or by the clubbing

together of bachelors or birds whose mates are sitting, or by the aggregation of newly fledged young simultaneously deserting their parents to form bands exclusively of the one year, or by the fortuitous concourse of all generations and sexes, deserves to be attended to in detail. Some flocks are freshly formed each day, and recruits can be watched joining the original members at intervals until it snowballs up to its full size. There is room for much work on the manifestations of this curious impulse in all birds which are in any way affected by it.

The local distribution of many species is exceedingly patchy and irregular; in some places they are common and in others, apparently of the same sort, they are entirely absent. There must be some reason behind this peculiarity, although none has been detected except in a few isolated cases. Often it may be due to competition, as has already been suggested, but that does not seem likely to explain nearly everything. Some work recently begun by the Oxford Ornithological Society suggests most strongly that geological conditions, acting no doubt through their influence on plants and invertebrates, may frequently be at the bottom of the mystery.

"The homing instinct" in birds has been the subject of a good number of experiments, many of a rather half-baked kind, but it has been little advanced by any of them, with the notable exception of the set conducted by two American scientists, Watson and Lashley, with sooty and noddy terns on Florida Keys. There seems no doubt that many, or perhaps all, species have a marked capacity for finding their way home over land or trackless water which they are most

unlikely ever to have visited before. This is especially conspicuous in the case of long-distance migrants which very commonly, though not always, return each breeding season to their native place, however freely they may have wandered since leaving it. But some preliminary experiments at the Oxford Trapping Station during the spring of 1928 showed that such a sedentary species as the greenfinch will return in a considerable number of cases from at any rate up to about nine miles in any direction. In the case of wild birds which have acquired "the trap habit" and are constantly being retaken, conditions are very favourable for testing—by removing them in closed receptacles to a suitable distance—how soon they will find their way back, if at all. But such work requires great care lest any point should prematurely be considered proved, and unless the experimenter is prepared to study the literature in order to learn what errors his predecessors have fallen into, and what difficulties they have met, he is unlikely, however much trouble he takes, to make any fundamental advance. Tests of bird intelligence are equally desirable on a large scale, but equally full of pitfalls.

It always seems curious to an ornithologist that so few ships' officers have taken up the study of birds with any enthusiasm. Very little accurate work is done at sea, although precise details of the distance from land at which various species occur, and anything throwing light upon times, seasons, or directions of migration would be of great value. It seems incredible that when the subject of birds crossing the Atlantic is of such scientific importance (at least half-a-dozen marked birds having already made the passage)

and at the same time of so much popular interest, that a bird can come aboard a liner which contains hundreds of unoccupied people, in mid-ocean, and be identified as a "duck" or a "sea-gull," as so often happens. The habits, food, and sometimes even the distribution of many birds found at sea are very inadequately recorded, and, of course, full details of any land bird occurring out of sight of the shore ought always to be noted. Even if there is no member of the crew with any interest in ornithology, some accurate standard work or a handbook like Alexander's *Birds of the Ocean* would insure that interesting migrants which actually rested on the ship should usually be satisfactorily identified.

The struggle for existence among birds is still remarkably obscure, and although the subject is by no means one of the easiest, any intelligent observer who concentrated upon it, in whatever part of the world, would be reasonably certain to discover something of value. He should devote his attention to accounting for the fate of the large surplus population which is usually in existence at the close of a breeding season, but has vanished, or been greatly reduced, by the middle of the next. He should try to ascertain what agencies operate on a large enough scale to have any definite influence upon the course of natural selection. For although it is assumed that large numbers of specialised characters are developed and kept efficient by a natural selection which ruthlessly weeds out those individuals in whom they are feeble or absent, yet, so far as birds are concerned, almost all this theory rests upon pure assumption. The work which ought to have been done to test in the field the Darwinian

hypothesis and its later corollaries, has not yet been set in hand. There is reason to believe that, however sound the theory may be in its most general terms, the nature of its special application to the living bird has been considerably misunderstood.

Enough has been said to show that the assertion that nothing remains to be discovered in ornithology is not entirely justified. In fact, if "everything" were substituted for "nothing" it would not be quite so wide of the mark. In this chapter only certain already apparent aspects of some of the more obvious problems with which we are confronted at the present time have been touched upon. If any attempt were made at completeness this little book would grow extraordinarily long, and it has to be remembered that in ornithology the solution of each problem reveals the existence of several others behind it. But no doubt any reader who may feel stimulated to play a part in the building up of ornithological science will find ample occupation for his energies among the lines of research just been pointed out.

Before leaving the subject of observation something must be said about ways and means. No costly apparatus is required, and the outfit of an observer is mental rather than mechanical, to be gained through practice and concentration instead of by monetary outlay. A pair of good field-glasses are the one article of equipment, not perhaps, indispensable, but at any rate valuable in most ordinary circumstances. While their pattern and power is to some extent a matter of taste and expense, probably the most serviceable for the normal observer are prismatic binoculars (which have a wide field of vision and good stereoscopic

quality), magnifying either six or eight diameters. There is little to be said for a lower power than 6x. The inexperienced observer is more tempted to choose the highest magnification he can afford to buy, but it has to be borne in mind that bird-watching is liable to involve the use of glasses for long periods at a stretch, and that unless the eyesight is exceptionally strong or the hand exceptionally steady anything above (or perhaps including) 12x will be found impossible to use without a cumbersome tripod. Moreover, the field at a thousand yards shrinks in proportion as the magnification increases, and binoculars which may be ideal for regarding a fixed object at leisure are often found to be less suitable for picking up a flying bird against a sky background. Some observers who devote much time to waterfowl and other not very restless forms, use a telescope to supplement an ordinary pair of glasses where the circumstances are appropriate. For the binoculars a leather rainguard fitting over the eye-pieces is valuable in most extremes of weather. Climbing irons in the case of difficult tree work or waders for marshy ground are almost the only other special things which the ordinary observer is likely to need; canvas "hides" are not commonly used by field ornithologists, except by bird photographers, although results might in some directions be improved if they were.

One thing remains more important than any of these paraphernalia of observation; an observer may do without field-glasses, but he can never do without a notebook. Most people have their own ways of taking notes, which are more often bad than good. To rely on odd scraps of paper and a pencilled scrawl is

nearly as bad as neglecting to keep any notes, and often more confusing. Some notes should be made in the field, but how fully depends entirely on the memory of the person concerned and other considerations, such as practice and the time which is going to elapse before they are copied into something more permanent. The permanent repository of notes should not take the form of a diary, or it will get out of hand as time goes on, and the references to any required subject will be very hard to trace. Something like a card-index or a loose-leaf ring-book is very much more sensible; it should have not only a heading for every species seen, but special headings for any particular point or group in which the observer is interested.

The final goal of the successful observation is that it should be published in the appropriate scientific journal of the country to which it refers, or to which the observer responsible belongs. In studying such literature, however well it may be edited, one is struck by the diversity in style, method, and outlook between the various contributors. Some hasten to send in their most trivial notes, others through diffidence, idleness, or too great caution fail to report things which are really significant and interesting. Some are terse, others verbose; some confine themselves to strict essentials, others allow themselves irrelevancies which may turn out of value to a worker on quite a different track, but this type is liable to leave out the essentials altogether. Some are very guarded in their identifications; others, and these perhaps the best, are a little apologetic and inclined to enumerate in detail the grounds for their decision; others are dogmatic and

peremptory. Some writers are controversial, going out of their way to provoke an exchange of brickbats, others are most careful to say nothing which could possibly offend anyone of any age or opinion. This diversity arises partly because ornithology as a science has still to find her feet, partly because ornithologists are for the most part amateurs (in so far as they are ornithologists and not professional bird photographers, writers, shooters, protection officials, or collectors) and are rarely trained scientists, but largely, of course, from a fundamental diversity of temperament. Almost the only thing that ornithologists have in common is that they never agree; whoever has taken any part in handling a British bird protection Bill will recognise that this is no smart paradox, but a mournful statement of fact, which must be faced in a later chapter. Amongst all this diversity of model it is clearly difficult to discover the true course. One thing is certain, that however much one indulges in swift provisional identifications in the field, no record should ever be sent in which stands the slightest risk of being overturned. If any doubt exists, always say so; it is better to point out an uncertainty over an identification oneself than to have attention called to it by somebody else. Moreover, the credit of any observer must depend very largely upon what he prints, and to be convicted of a blunder cannot fail to be a shock to it. In the field, on the other hand, although personal practice differs, it is quite legitimate among an unfamiliar avifauna to use tentative diagnoses, even if they are very likely to turn out wrong. It is easier to call something with definite characters by a name than to call it X, and a theory

of its true identity is easier to prove or disprove than a vague confession of agnosticism.

The ideal at which an ornithologist should aim is clearly that he should record sooner or later everything in his notes which is worth recording and nothing which is not. This implies for every observer a much better standard of values and a wider acquaintance with what others have already done than is usual at the present time. On the whole, observers do not read nearly enough about birds, at any rate of a fruitful sort; if they read more they would be able to observe to better purpose and to record with greater confidence and knowledge, so that through being more in touch with the main stream of ornithology they would contribute more largely to it.

CHAPTER V

BIRD-MARKING

THE old-fashioned ornithologist was an individualist; and, as we have seen, there is a great field for individualism still. But the most striking feature of twentieth-century ornithology is the sudden rise to importance of organised co-operation. The first aspect of this movement to be considered is the growth of bird-marking. Marking in a crude form was practised occasionally in the eighteenth century, if not earlier, but it was first systematically employed with young woodcock on the Duke of Northumberland's estates at Alnwick in 1890. Very soon afterwards Mortensen began to develop it in Denmark with a scientific ability and success which has never since been surpassed. During the first quarter of the twentieth century other schemes sprang up all over "Nordic" Europe, and among the Slav nations it was pursued with conspicuous energy in Hungary and to a less extent in Russia. Very recently France has taken up ringing. There have been two or three British marking schemes, which were wound up some time ago, but much the most considerable, and the only one at present in operation, is the *British Birds* scheme conducted by Mr. H. F. Witherby. This has a large, though fluctuating, number of "ringers" working for it in many parts of Great Britain, and had succeeded from its inception in 1909 until the close of 1927 in dealing with more

than two hundred thousand birds. On the other side of the Atlantic "bird-banding," since it was first organised in 1920 by the Bureau of Biological Survey (a part of the United States Department of Agriculture), has undergone expansion on a typically American scale, so that it has now taken first place in point of numbers ringed annually, averaging at the present time about seventy thousand birds a year. This has also the distinction of being the only international effort in what should be an essentially international form of research, for Canadian as well as American observers take part in it.

Although a considerable variety of marking methods have been tried at one time or another, only the light metal ring has proved satisfactory. It is necessary that the medium used should survive as long as the bird which bears it; that it should carry a legible number, so that the individual history can be traced, and a legible full address for the finder to communicate with; and, finally, of course, that it should in no way hurt or inconvenience its bearer. Certain other methods which fulfil the last three conditions fail to comply with the first, so that the most interesting long-period records are most tantalisingly lost; it is difficult to find anything except the strip of aluminium alloy which can be readily bent into a regular ring to slide up and down the leg, and is at the same time light enough for the bird and durable enough for science. Nor is there much scope for variety in conditions of use. "Rings," or "bands," are usually issued in packets of ten or twenty consecutive numbers, accompanied by blank forms or schedules to be filled up as each one is used. These schedules have separate spaces or columns in

which are entered the date of marking, the number of the ring, the species marked, and, wherever possible, the sex and age (that is to say, whether adult, immature, or nestling), and the locality, together with the name of the marker. Most rings can be manipulated easily by hand, but a few demand pliers, and the larger sizes—for they are issued in different grades suitable for different birds—are often fitted with a clasp. At the end of each season, or when operations are finished, the completed forms, together with a list of birds marked, are sent in to the organiser of the scheme, who files them and sorts out recovery records accordingly.

Marking has been done, with surprising success, on a purely chance basis, the birds being released in the pious hope that at some other stage in their career, and most often at the end of it, they will again come to the notice of some human being who will see the ring and communicate with the address stamped upon it, giving details about its number and the place and date of recovery. If possible, its species and fate should be added, although the species can always be traced so long as the number is known. It is, of course, impossible to tell how many people who find marked birds fail to report them, but a great many are reported, the percentage varying from 0·1 per cent. in the case of very small short-lived species ringed in Great Britain to as much as 20 per cent. for Danish-ringed duck. Naturally, the recovery percentage is by far the highest in the case of birds which are much shot for food, or as supposed enemies to certain human activities. It is a not uncommon belief that there are men particularly on the look-out for ringed birds in order to shoot them.

This, of course, is entirely without foundation; successive recoveries are of such extraordinary value, as compared with single records, that no serious bird-marker would be willing to destroy the chance of them in this way, even if he were able. Moreover, a worn and tarnished ring is so nearly indistinguishable at any ordinary range, and the proportion of marked birds to the whole population always so minute, that any such scheme would be impracticable, even if anyone wanted to attempt it. As no bounty is commonly offered for the recovery of a ring there is certainly no inducement to the chance gunner to slay in the hope of securing one.

Yet the question of increasing the percentage of recoveries, and so making bird-marking more fruitful, is naturally one in which ornithology is interested, and the United States has given a lead in this direction by the establishment of a considerable chain of privately operated trapping stations scattered over an immense territory. It is one point of contrast between the New and Old World schemes that in America most of the birds marked are adults, but in Europe they are nestlings. Nestlings, of course, are easily caught and marked without any special apparatus, and have the notable advantage that a subsequent recovery is likely to throw light on their longevity, their return to the native place, the winter quarters of different birds from the same locality, and any cases of settling down to breed in a different country from the native one. In this respect the American system, which discourages the banding of fledgelings, appears open to criticism. On the other hand, marking of nestlings is wasteful, because so much of bird mortality occurs in the first

few months of life. Trapping is a notably economical method and gives a much higher recovery rate, since the marked individuals tend to remain in, or to revisit, the same locality, and a single bird may enter the trap fifty or a hundred times. There is, of course, a good deal to be said for and against each method, and it is probable that each is superior where it proves successful. In America, where predatory animals are much more likely to follow the trail of the observer to the brood which he has just marked, and where the ratio of human to bird population and the area of operations is on such a different scale, it is evident that concentration on nestlings is quite a different business from what it is in the British Isles. Moreover, the greater extremes of American climate tend to make trapping more efficient and fruitful than it is in the moist and mild English winters with their briefer spells of frost. Trapping can, of course, proceed at almost any season, but it is certainly most productive during severe weather.

When bird-marking was started, the migration question, largely through Gätke's fantastic dogma of 1890 that a small bird could cover long distances at well over two hundred miles an hour, was much more prominent than it is now, and, consequently, it was the obvious usefulness of ringing as a means of tracing journeys which led to its being so widely taken up. But the more bird-marking is practised, the greater its potentialities are seen to be. In summarising these various branches of its usefulness, it may be well to give a few examples of the sort of records that have already been obtained.

In the obvious sphere of long-distance migration there is a whole set of striking records. The Atlantic

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is known to have been crossed by marked European birds on five occasions—twice by kittiwakes from England, twice by black-headed gulls from North Germany, and once by a Lake District lapwing—and from the American side once—by a common tern banded in Maine and recovered on the delta of the Niger. Greenland kittiwakes have been taken on both the European and the American side. A hundred white storks marked in Germany, Denmark, and Hungary, have been found in various parts of Africa, mostly down the east coast, and seven British-ringed swallows have occurred there, one on the Congo and six in the extreme south-east. Terns from the United States, including some of the more northerly parts, have occurred in the West Indies and South America; a Kerguelen albatross has been taken near Cape Horn after a seven thousand mile journey; and widgeon from England have occurred in East Russia.

Although spectacular, these records are at present too isolated, with one or two exceptions, to allow any very definite conclusions. But the masses of data which have been obtained are beginning to give a very clear picture of the movement of some abundant species between their summer and winter quarters—of the migrations of gulls, duck, hooded crows, rough-legged buzzards, and starlings from the Baltic countries; of lapwings, thrushes, duck, snipe, and many others from the British Isles; of grackles, gulls, duck, Canada geese, American robin, and others from North America. Of these the American results are, in some ways, the most interesting, being concerned with a large uninterrupted continent stretching through many degrees of latitude and a variety of climates. The manner in which some

species spread out fanwise from a compact winter quarter by the Gulf of Mexico over summer territory covering almost the whole width of North America seems particularly striking. Unless further data materially differ from those already issued by the Biological Survey in December, 1927 (Technical Bulletin No. 32 of the U. S. Department of Agriculture), the isolation of California and the Pacific coast region, which shows remarkably little interchange of population with the remainder, must also be ranked among the important facts of distribution which only bird-marking can bring out.

Longevity is one of the aspects of the life of a wild bird about which until very lately we knew nothing in particular. Even records concerning captive specimens are not nearly so abundant or accurate as one might expect, and the difference in diet and environment is generally such that they form a particularly treacherous analogy. But ringing, where it takes place on a sufficient scale, and the recovery rate is reasonably high, does allow us to form some idea of the length of a bird's life. When great numbers of American purple finches, juncos, "sparrows," catbirds, and chickadees (these last being conspecific with the European willow tit), or of European robins, finches, hedge-sparrows, buntings, and so on, are retrapped over and over again up to the end of their second or third year, and then much more rarely till after the sixth none occur, it seems a reasonable conclusion that the great majority must live only up to three or four years old. Some of the larger birds, however, seem frequently to reach ten or twelve years old, including the lapwing, heron (which has been recovered in its

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sixteenth year), and various birds of prey—large gulls and duck. Although the newness of the American scheme makes it necessary to wait a few years in order to be certain, it seems that the expectation of life for a duck in America must be less than half what it is in Europe, owing, no doubt, to the immensely greater number of "hunters" on that side. The invariably low age at death shown by the latest American returns for this group is, at any rate, an indication of a way in which marking can help to supply data for the protection of game-birds on more scientific lines.

These are all aspects in which a great mass of results is necessary as a foundation to any reliable conclusions, but there are other directions in which ringing may be used to trace the life of the individual bird. By marking British robins with coloured rings, which rendered them distinguishable as individuals in the field, Mr. J. P. Burkitt has been able to discover a great deal about the mating and territorial relations, and the local movements of a most interesting species. It is clear that a considerable amount of similar work remains to be done for this and many other forms. To trace the pedigree and fortunes of one or more families through several generations is an obvious instance. A series of remarkable examples in Britain and North-Western Europe show that duck, and perhaps other birds which are native to one country, may "abmigrate," and be found breeding in another, up to thousands of miles away. Only the numbered ring could have brought this fact to light, and, as Mr. H. F. Witherby has pointed out, it may have an essential bearing upon the conspicuous absence of geographical race-differentiation throughout the group. If the stock

from one part of the range persists in interbreeding with the stock from another, it is clearly improbable that any divergence of type can occur.

As a final instance of the usefulness of bird-marking in unexpected directions, a raven casting found on the Oxford Expedition to Greenland in June, 1928, proved on analysis to contain some berries and remains of a daddy-long-legs, a humble-bee, and some small chick, together with a mangled but still just legible ring, which identified it as one of a brood of newly hatched purple sandpipers marked by a member of the Expedition a few days earlier within a mile of the same spot. Here the date of the casting and the identity of the victim could hardly have been discovered but for the presence of the ring.

Although it suffered a considerable set-back during the war bird-marking is now in the most flourishing state that it has ever attained to, and if the present rate of growth is kept up results on a really satisfactory scale ought to be forthcoming within the next ten years. Besides being one of the most potent of our methods of research it has the advantage of offering some opportunity for all who take an interest in ornithology to be of some service to it; either by acting as ringers themselves, or at least by being always on the lookout for recovery records, and by making the scheme familiar to all who are likely in the course of their occupations to meet with any marked birds.

CHAPTER VI

THE BIRD CENSUS

SOME of the fundamental problems of bird life resolve themselves, upon analysis, into simple questions of numbers. The proportion of birds of prey to their victims, of any species to its competitors, and of the population as a whole to the food resources at its disposal, have a vital bearing on the economy and social organisation prevailing over a given area. We find by observation that the behaviour, even what we should have considered the psychology, of birds, alters in accordance with the density of population; they tend to be more truculent and quarrelsome where there are many in relation to the quantity of food or breeding space, and more tolerant where the pressure is lower. Both the territory theory (which traces how towards the breeding season many birds become strict individualists, claiming a private domain from which all others of their kind are rigidly excluded), and the study of economic ornithology (which is the indispensable basis for rational bird protection), demand a great deal of accurate census work before they can progress much further. The conditions governing the increase of communities, or of birds in any stage of organisation, are largely matters of statistics. In the last thirty years, therefore, line after line of observational research has found itself brought to a check, and has been forced to make some attempt to pro-

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vide itself with numerical data in order to go forward again.

The growth of bird census work has been rapid and cumulative. Until the war very little was done, and that mostly in the United States and Germany. The United States Bird Census, organised by the Bureau of Biological Survey, remains the only national effort which has anywhere been made towards enumerating bird population as a whole. But it necessarily involved calling upon a good many observers unsuitable for such skilled work, and the use of rule of thumb methods, so that the isolated studies carried out elsewhere, particularly in Great Britain, often reach a higher standard of accuracy. It is doubtful whether as lately as 1925 there were above half a dozen persons engaged in scientific bird census work anywhere in the British Isles. By 1928, chiefly owing to the census of heronries undertaken in that year through *British Birds*, the number had risen to at least three hundred. At Oxford a corporate scheme of research has been in operation since 1927, but many more observers will have to be set working before the future of this investigation can be considered assured, and before data are available on a large enough scale to be of any permanent importance. While much excellent work has been done in America it is probably not unfair to say that the immediate need is to raise the quantity of census work in the Old World and the quality of it in the New.

A census may take several forms. It may be carried out by a single man on his own, or by an organised group repeatedly working the same limited area in order to secure comparative figures, as has been done

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on the Oxford University Farm, or by a central office directing a number of observers scattered over the country. Its scope may include all the birds, of whatever species, which inhabit a patch of comparatively small extent; or it may be restricted to a single species or a small number of species, of a suitably conspicuous sort, and cover a much larger area, like the complete census of rookeries done in 1928 by Roebuck throughout Nottinghamshire, Derbyshire, and Leicestershire, or by the Oxford bird census over 224 square miles in the neighbourhood of Oxford. If the species is not too abundant and otherwise well fitted for it, the scope may be national, and the entire breeding stock of a given bird in a given country be made the object of inquiry, as was done in the *British Birds* census of heronries, and in Holland for the same species by Brouwer in 1925.

These different varieties of census are not only subject to different methods, but are directed towards different ends. A count of a single species over a large area is particularly bound up with an investigation into economic status (and of course into protection also, for the two are hardly separable). It will aim at bringing out any striking change in numbers or distribution, and when linked up with the results of an analysis made from an adequate sample of stomach contents (and castings, where those occur) it will be able to show with fair accuracy which sorts of food are consumed by the subject of the inquiry, and in what quantity. Thus, in the hypothetical case of a conspicuous bird which fed simply on corn, it would be possible to ascertain how much corn each individual got through in a week, and, by multiplying up to the

number revealed by census work, to show just how many bushels' toll were levied by that particular species. In practice, of course, there would be alternative forms of diet, some of which might work out in the interests of agriculture, and the proportion of each food consumed would vary at different seasons; such factors would complicate the problem, but they would not render it insoluble, provided the spade-work done on the census and in the laboratory were thorough. There is, however, an alternative reason for counting one species over a large area; such a species will probably be so wide-ranging, or communistic in its organisation, or both, that a complete bird census on any feasible scale cannot hope to do justice to it. The practice of including strong breeding colonies in a general census without their foraging grounds is much to be deprecated, since it can never give a true picture of the real density—that is to say, the ratio of bird population to the whole area supporting it. In any case, where this has to be done, the density should never be stated without the abnormal condition being pointed out. In a census where an area is first chosen and then all the birds upon it are counted without exception, the aim will be not so much to elucidate economic status, but to establish density, fluctuations, and the effects of competition, or if it is sufficiently intensive, to investigate the relations of each pair to their territories and to one another. The detailed study of a small piece of ground is also valuable for bringing to light all sorts of intricate and often substantial local movements which might not otherwise be suspected.

A further type of census, less ambitious but useful

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in the absence of more thorough work, is the arbitrary cross-section through a wide extent of country. It may be carried out on foot, and may take the form of a transect of mountain-slopes through the various animal and vegetable zones, such as has been done by the present writer in the Alps from about 2,500 to 10,000 feet elevation, or of a count from the train, or from a ship at sea. In any case it is indispensable that the distance over which the count was made should be recorded, together with the time of day, weather, speed of motion, and anything else likely to have affected the figures. A division into sections is often convenient.

The accuracy of a bird census varies greatly according to the conditions of site and avifauna, and the experience of the observer. For a single suitable species, or for all species over a sufficiently open area of up to about ten square miles as a maximum, it may probably be brought within an error of two per cent. with the aid of a double check. Generally speaking, the proportionate error will diminish as the size of the area undertaken increases, up to the point where it begins to pass beyond the observer's power to keep pace. The explanation of this fact is that transient visitors, and overlapping of boundaries, are a much more serious matter in a small area than in a large one.

It is in many ways a misfortune for the development of the bird census in Europe that there is no sort of central body interested, or in any way responsible for it. Obviously there has to be, if not rigid control, at any rate some form of general guidance if the most is to be made of opportunities. Observers need direction,

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and must be prevented from overlapping unnecessarily; without some recognised clearing-house it is going to be hard to make the data which have been secured available where they are needed, since their publication, even at this stage, would inundate all the available scientific journals to an impossible extent. Moreover, it is essential that there should be some standard laid down, so that results may be made comparable; not only laxity on certain points, but the mere use of a diversity of methods, however good in themselves, will seriously detract from the value of the work done.

CHAPTER VII

BIRD PROTECTION

It is agreed in most civilised countries that birds, or at any rate some of them, ought to be protected against human persecution. But in spite of international conventions no sort of agreement has been reached in practice upon the protective measures which ought to be taken, or even the principles upon which they should be based. Canada and the United States have an understanding with regard to migratory species, but repeated efforts to secure something of the same kind in Europe have always come to grief. One of the most backward of all countries is Great Britain, where legislation which ought never to have been passed (and which everyone concerned has been trying for at least twenty years to repeal) remains nominally in force, owing to the irreconcilable differences of opinion, not only among interested parties, but among ornithologists of all kinds. These differences of opinion are due to the fact that while most of those concerned have met with the problem, and have thought out a specific remedy for particular evils, few or none have gone into the principles of sound bird protection, or attempted to obtain the data necessary in order to know the precise status of the forms to be protected.

It is clear that protection may be based upon a variety of ideas. It may, for instance, be based on

economic usefulness or the reverse. In that event, unless the law is to be drafted simply according to the prejudices of ignorant and interested classes, it will be essential to inform ourselves beforehand on the facts which are to determine the legal status of each species. That is to say, we must have, instead of a handful of stomach contents with large quantities of opinion and hearsay thrown in, a complete investigation covering all parts of the country and all seasons; reinforced by a reliable census telling us within a reasonable margin the actual numerical strength of the species with which we have to deal. Or protection may be based on the idea of compensation. It may represent an attempt to counteract the effects of human encroachment by safeguarding the surviving stock of the species affected, forbidding interference with their nests and eggs, and, possibly, where their breeding area is compact enough, setting aside a sanctuary or reserve for their benefit. In England, so far as any principle at all has been followed, this has proved much the most popular. It has the advantages of not demanding any action until the eleventh hour, of providing repeated opportunities for exploiting the sentimental aspect, and of enabling various rather decrepit and more or less well-meaning societies to pose as the apostles of bird protection, without making themselves unpopular among any section of their supporters.

It hardly needs a scientific investigation to show that a bird which has fallen from general abundance to a mere handful of pairs is in need of special protection. But it is always assumed, and not always with justification, that the regulation of deliberate

human interference must necessarily make some difference to the numbers of the species involved. It is from that standpoint quite useless to protect any form which has not hitherto been suffering from persecution. In most countries there are a great many small birds which nobody takes any notice of; to put them in a statute may look well, but it will not affect their numbers, because man is no more than a negligible factor among their enemies. There are, in fact, probably comparatively few species, except among certain Latin nations, which are capable of being appreciably multiplied by the grant and enforcement of the most generous protection. A few finches which are coveted by bird-catchers; a few farm pests, real or supposed; a few which are shot as enemies of game or fisheries, and those which interest the wild-fowler will probably exhaust the list.

There are, of course, other methods of protection besides the mere prohibition of destruction. Not only enemies, but a shortage of nesting-sites, of water, or of food may be the principal obstacles to expansion, and measures to remedy any defects of this sort may lead to a spectacular rise in the bird population, such as has been seen locally in many countries, perhaps most notably in Germany and the United States. It is a question how far such artificial stimulation is desirable in the long run. To put down food on a large scale in the nesting season, as is said to be done in America, is clearly an unwise system, since that season always more or less coincides with a more than average abundance of natural food. To supplement these resources, if it has the desired effect of increasing the breeding stock, must lead either to artificial feeding

on an even larger scale during the remainder of the year or to a most appalling discrepancy between the number of birds reared and the number which have any prospect of survival. Moreover, the moment such methods are adopted, the psychology of poultry-farming begins to enter into the situation, at any rate on the human side, and we find an almost irrepressible itch to destroy any species of predatory or parasitic habits which is seen to harry the carefully fostered community. The result, unless some extraneous factor can avert it, must be to bring about such a density with so low a standard of selection, that the latent parasites will soon get out of hand, and a terrible mortality will sweep through this artificial community, leaving it in a thoroughly enfeebled state and far below the normal level of numbers from which it aspired to enfranchise itself. The perils of this sanctuary system of protection are not sufficiently realised in England, and apparently still less in America; far-seeing bird protection must aim at a stable population living under natural stresses and not at a pampered community temporarily released from their operation, only to suffer in the long run a disastrous-retribution.

The supply of water, on the other hand, simply remedies a chance natural defect confined to a very limited area, and seems open to no objection; while nesting-boxes and other artificial breeding-sites, although they tend to avert an undoubtedly healthy competition, can be furnished in any reasonable numbers without any apparent risk of undesirable consequences. Erection of nesting-boxes, planting of suitable cover, and other measures to enable birds to breed without unreasonable disturbance, seem, in fact,

to be the only legitimate scientific means of increasing a bird population which is already immune from human enmity. Certainly such methods do not involve any short-sighted tampering with the check imposed through the food supply, or through the activities of birds and beasts of prey. The gun is never a defensible weapon of bird protection, except in such very extreme cases as when the meagre remnant of some small, weak species is faced with imminent extinction, and is clearly suffering severely from the presence locally of a strong natural competitor or enemy. But any system of bird protection which logically leads up to the shooting of some forms in order to multiply others is clearly on a par with game-preserving. This point was emphasised in the present writer's *Birds in England*, published three years ago, and has nowhere been contested, although a large number of bodies responsible for bird protection in all parts of the world continue to act contrary to the true principle in their everyday practice. To bring bird protection, both in its legislative and popular aspects, more nearly into line with the findings of ornithological research, is one of the most urgent concrete tasks to be taken in hand by students of bird life.

Protection in most countries is a matter partly of law, partly of sentiment, partly of interest. To take some English instances, the lapwing and the great-crested grebe owe their protection, so far as it is effective, mainly to the force of law. Convictions for shooting them are probably frequent enough to form a certain deterrent. The robin and swallow, on the other hand, are much more powerfully defended by a

deep-rooted sentiment, and by public opinion, than by any legislation applying to them. To be known as a killer of such birds would in most cases involve a very real unpopularity, which few would care to incur. The pheasant, on the other hand, would get short shrift but for the power of the interest behind it, which controls not only the local magistracy sitting in judgment upon offences against the game laws, but the local economic community to which most potential offenders belong. This, of course, is an instance of a bird protected from slaughter by some people in order to be slaughtered by others, but in some parts of the world there are instances of an interest requiring the absolute preservation of certain species, like the secretary bird of South Africa or the carrion-feeders of certain tropical and Oriental cities.

In considering bird protection it has always to be borne in mind that a species can never be isolated from the natural association or community of which it forms part. Thus, there are communities of farm-birds, of woodland or forest birds, of marsh birds, of shore birds, of ocean birds, and many others in all parts of the world; and each of the members of these is to be judged not only by what it does itself, by direct consumption and otherwise, but by the part it plays in maintaining the general balance. Thus it is quite possible for a bird to be exclusively harmful, judged by its food analysis, and yet deserving of full protection owing to the much more serious evils which its extirpation would induce, and, of course, *vice versa*. We hardly possess full enough knowledge yet for definite examples, but the case of the starling, which has now become definitely more injurious than

beneficial at certain seasons in many parts of the United Kingdom, while appearing quite obviously beneficial in the United States where it has been introduced, will give some idea of the complications involved. If, as seems possible, the starling and some other species begin as useful birds but, multiplying rapidly, change their diet and become a pest, then it might be advisable to nip such an introduction in the bud, provided that would save native species of less prolific and omnivorous tendencies, which could be trusted to maintain a steadily beneficial economic status.

The general principle which seems to emerge, so far as present information allows us to come to any conclusion, is that instead of trying simply to protect birds we know to be useful, we should protect all except those shown to be injurious, with, of course, some seasonal suspension in the case of forms which are locally reckoned as game. Few protection enactments have hitherto shown the essential merit of simplicity; the law must be clear, for it is inevitably a law which closely affects many uneducated people, and it cannot be expected to work well unless they can understand it. For any other country but England, it is perhaps unnecessary to add that protection ought to be national in its scope and that a series of orders differing completely in every county will be childishly simple to evade. That does not, of course, rule out the temporary and local suspension of protection in the case of a single species or group wherever for some reason it is considered desirable, but on the whole the basic legislation should apply without discrimination between one district and another. Some means

will have to be found of exempting from penalty birds-nesting by schoolboys, wherever it is at all widely practised, and licences will have to be granted in carefully defined terms to genuine students pursuing a line of research which demands special facilities. With these exceptions, the protection of nests and eggs of all species not expressly black-listed will have to be rigidly enforced, until the destructive and unjustifiable money traffic in stuffed birds and egg-shells for private collectors, and the haphazard destruction of rare forms from ignorance or hope of profit, has been effectively suppressed.

Bird protection, if it is to avoid serious reverses, must not aim at unduly increasing numbers, except where they have demonstrably been reduced. It must set out to salvage species whose existence has been put in jeopardy by the squandering destruction of the last six or seven generations, to preserve a normal and enduring balance of nature, to simplify the task of the observer, and to increase the pleasure of all and sundry by gradually removing the lack of confidence which birds feel in mankind.

CHAPTER VIII

THE FUTURE OF ORNITHOLOGY

THE more one considers the ornithology of the past the more one must turn to the future. With so many problems exposed and so few followed up, so much set in hand and so little conclusively achieved, it is natural that a wide acquaintance with bird literature should lead to incessant speculation on the course of this curious science, and an impatience to remedy the lack of data which is everywhere making its starving influence felt. It is clear that ornithology is now, and always has been, so short-handed that adverse criticism of its efforts may seem distinctly ungracious, yet, on the other hand, it enjoys as wide a popular interest as almost any branch of science and the number of potential observers who might be enlisted is colossal. Practically all this potential assistance is allowed to run waste because ornithology has never possessed the means of harnessing it, and because so few, even amongst those who are called ornithologists, have any clear vision of what needs to be done. The immediate necessity is not so much to expand the ranks of the observers as to direct into more profitable channels the energies of the not inconsiderable number of observers who are already at work.

The day of the individualist observer as the typical, and almost the only, representative of ornithology is undoubtedly past. He may, and certainly should, have

a glorious future in store for him. We have reviewed in a previous chapter some of the lines of research which still await his attention, without attempting to be exhaustive, or to deal with such important and absorbing subjects as courtship and display, and the intricacies of the territory theory. These are too complex for treatment in a work of this scope, and are dealt with in some of the works cited in the Bibliographical Note (page 77). As an experimenter, also, he has a wealth of unexploited opportunities, but here, owing to the number of traps for the incautious, trained scientists must usually enjoy a monopoly. The work which is being done by Rowan in Canada on photo-periodism as a factor in bird migration, or by Thienemann in Germany in narrowing down the migratory impulse in storks, are indications that the possibilities of controlled experiment are not being altogether neglected.

The individualist in the future must be only a part of the strength of ornithology; there must be a large and sufficiently organised corps of observers, co-operating for the solution of definite problems laid before them by some central directing body. In America the United States Biological Survey has undertaken these duties so far as it has been able, and the success there met with serves to show up the chaos in the European countries. It is almost incredible, in view of the great economic importance of birds and the light which their study can throw upon other obscure aspects in nature, that there is still no Institute of Economic Ornithology in the United Kingdom, nor even any endowment at any university to assist the study in any way. Hungary, which is not

considered a violently progressive country, has possessed such an Institute for a long time, and it is obvious that until the Ministry of Agriculture, or some private fund or persons, rise to the occasion by founding some centre for ornithological research in the British Empire, little progress can be made towards the co-ordination so urgently required. Even if other European countries establish centres on their own, they cannot secure the help from British ornithology which they have a right to expect, until a whole-time, well-paid, and well-trained staff is in existence to guide the energies and digest the data of observers in the British Isles. An Institute, presided over by a competent ornithologist, but containing also an entomologist, an expert of agriculture, and another on plant ecology and botany—with some provision for keeping contact with forestry, research upon fisheries, and so on—would, provided it were directed with sufficient initiative, pay its cost over and over again by reducing the depressing waste and dissipation of energies characteristic of the present stage of ornithology, quite apart from the results which its special investigations ought to bring. That it should be left to private observers to face the gigantic business of undertaking volumetric analysis of stomach contents on a national basis is only less incredible than the fact that a few courageous investigators, notably Dr. Collinge, of York Museum, have been found willing to try their hand at it, albeit on so relatively small a scale that nothing conclusive can be hoped for until things are put upon a more reasonable footing.

Ornithology will have to organise itself, not as it has been content to do in the past, through friendly

societies better fitted for mutual admiration and pleasant converse than for any more active utility, but under working Institutes. One might be provided for each country, or, where circumstances permit, for each region or group of countries, each having, if not actual control, at least a very strong moral influence in directing the course of research, and in ensuring that the resources and energies at its disposal are used with the maximum effectiveness. This is not to say that all or even any existing bodies need be wound up or superseded, nor that the national supremacy which has been established by such associations as the British Ornithologists' Union, the American O.U., the Royal Australasian O.U., and so on, in their respective territories, ought in any way to be touched. The new co-ordinating bodies would be supplementary, and would restrict themselves to their obvious duties in the field of research; they might well be subordinate to the all-inclusive organisations which have just been referred to. The desirability of having an authoritative clearing-house for observers, such as is formed by the British Museum and similar institutions abroad for systematists, is so obvious that such a development would be as likely to receive a general welcome as anything new in ornithology could expect.

It will be necessary also to undertake a vigorous campaign to shake the local natural history societies and field clubs out of the apathy into which they have mostly sunk, and although this applies particularly to Great Britain, it is true also of other countries. Too many of them have fallen into the hands of an elderly and passive group of amateur naturalists with obsolete ideas and next to no initiative. For this the younger

members are often largely to blame, since they have displayed remarkably little initiative themselves. Almost all societies, even the busiest and the most urban, could undertake some limited but valuable scheme of corporate observation. If they would make the effort many could without much difficulty run an organised trapping station, requiring only about ten participants, of which at the present time there is only a single example in England. Many of these local societies publish transactions, or similar periodicals, the value of which is sometimes very small. It has been pointed out by Mr. Charles Elton that the best of the small regional journals are usually those associated directly or indirectly with some university or big museum, which suggests a line for future development. A good many existing publications of this sort might advantageously be combined.

The supply of future ornithologists should not continue indefinitely to depend, as it has in the past, on the chance of a small number of birds'-nesting boys growing up to take an interest in other aspects of bird life. School natural history societies ought to be in touch with similar associations both regionally and at the universities, so that leaving members who are sufficiently interested may readily be transferred from one to the other. The whole question of biological training is at present in a state of flux, owing to the fact that education has failed to keep pace with the recent expansions of professional biology; but there is reason to believe that the next few years will see a general revision at the expense of the older sciences, notably in the English public schools, and from such a development ornithology stands to gain. One of the

great obstacles which have hindered its balanced development as a science has been that almost all the paid posts concerned with it have supported only systematic and anatomical zoologists, who, working in their museums, have until quite recently been prone to ignore or belittle the observer in the field. Now that systematy is sufficiently cleared up for the balance to be shifting the other way, it ought to be possible to secure for research in the field something like the nucleus of trained zoologists which it needs. In this connection it is worth noticing that almost all the more fruitful observations for a long time (again so far as Great Britain is concerned) have been due to non-scientists. The territorial habits of the robin have been exposed chiefly by a county surveyor and a retired Cabinet Minister; most of the other work in that direction has been done by business men in their spare time. Although the results of this amateur research have proved remarkably good, those who have taken the chief part in it would be the last to deny that trained zoologists who have outgrown the old obsession with systematy and purely laboratory work will be a valuable addition to their ranks.

It is not to be concluded that the rationalisation of ornithology which has just been pictured will destroy the liberty of the private worker in any way. In fact, just as Man in the mythical State of Nature can have no rights, and therefore no real liberty, so the ordinary observer is inevitably tied down in a state of unimaginative bondage to the fetishes of an outworn conception, until some steps are taken to reduce the science to order and to clear for him a path which he may profitably explore. Ornithology has never

been so widely popular as now, nor so acutely conscious of her ignorance and her shortcomings. Given the vision, the energy, and the patience to direct her efforts in the right way, she is assured of a future very much more fruitful than her past; whether she will attain it without much spendthrift activity and unjustified delay rests with the observers of the present generation.

BIBLIOGRAPHICAL NOTE

THE bird literature of the world is a colossal subject, and in this brief note it will not be possible to cover, even in the most summary manner, anything like the entire ground. Having regard to the fact that this is primarily an English work, the majority of the works cited must be in English; this, however, is not altogether unrepresentative, since the majority of important publications in recent ornithology have been in that language. Further, since this little book is scarcely intended for specialists, popular expositions of a reliable but non-technical sort, especially those containing bibliographies, must have the most attention.

On the general biology of birds, a subject only to be tackled in a fairly large work with unlimited illustrations, some excellent books are available. Of these Professor J. Arthur Thomson's sound and lucid *Biology of Birds* (1923), from a European standpoint, and William Beebe's brilliant popular exposition in *The Bird* (1907), from an American, are the most to be recommended.

There is no history of the birds of the world, and only single groups have hitherto been at all exhaustively treated from a cosmopolitan standard. Among these William Beebe's *Monograph of the Pheasants* (1918-1922), J. C. Phillips' *Natural History of the Ducks* (1923-1926), and, as a pocket handbook, W. B.

Alexander's *Birds of the Ocean* (1928), may be cited as good recent examples.

Taking regional works, Dr. E. Hartert's *Vögel der Palaarctischen Fauna* (1903, etc.) has superseded Dresser's *History of the Birds of Europe* (1871-1896), but is written in German. For ordinary purposes, Wardlaw Ramsay's *Guide to the Birds of Europe and North Africa* (1923) is a very convenient work which will go in the pocket, but it has its limitations, is in some respects out of date, and on questions of distribution not remarkably accurate. The standard work on British birds is H. F. Witherby's *Practical Handbook of British Birds* (1919-1924), in which the level of accuracy is extraordinarily high, but the various plumages are given in so much detail that, apart from points of distribution, T. A. Coward's compact *Birds of the British Isles* (1922)—especially the first two volumes, the third being a somewhat disjointed collection of addenda—will be more useful to the ordinary observer. It contains a good range of fairly faithful coloured plates, and a good deal about habits; for the most complete treatment of these last, reference should be made to F. B. B. Kirkman's *British Bird Book* (1910-1913) which, like Witherby's, includes contributions from a set of leading specialists. Thorburn's *British Birds* (1926) is more of a picture-book than a comprehensive ornithology; the pictures, however, are often very good indeed. A marvellously cheap identification book, and much the best of its sort, is Kirkman's shilling *British Birds* (4th ed., 1928), in the "People's Books" Series. Naturally, the rarest forms are not included, but it gives everything at all likely to be met with, and the descriptions are terse and accurate. It is

clearly impossible here to attempt discussion of local avifaunas outside Europe, although good works exist, in more or less variety and detail, for most parts of the world. The various encyclopædic works on birds, such as volumes in the *Cambridge* and the *Royal Natural History* are generally good as far as they go; Professor A. Newton's *Dictionary of Birds* (1893-1896) is long out of date, and there is no current work covering quite the same ground.

For tracing references to local British avifauna *A Bibliography of British Ornithology* (1916-1917), by W. H. Mullens and H. Kirke Swann, must be considered indispensable.

The Origin of Birds, by Gerhard Heilmann, and *Problems of Bird Migration*, by Dr. A. Landsborough Thomson (both 1926), are thoroughly sound works on the subjects apparent from their titles. *Animal Ecology*, by Charles Elton (1928), treats from a general zoological standpoint the relations between various animals (including birds) in a social and economic sense; the same subject is treated purely ornithologically in the present writer's *How Birds Live* (2nd ed., 1929), which contains appendices summarising recently published and unpublished data, including bird census results. There is no book devoted to this last subject, or to bird-marking, although Landsborough Thomson (above cited) gives quite a good account of it incidentally. The only book on bird protection in the British Isles is the present writer's *Birds in England* (1926), which includes a fairly full account of historical fluctuations in status. *The Food of Some British Wild Birds; a Study in Economic Ornithology*, by Dr. W. E. Collinge (2nd ed., 1924-1926), represents very nearly the sum of

our present knowledge upon its subject. In America a very complete summary and bibliography of the subject has been furnished by Professor J. Henderson's *Practical Value of Birds* (1927).

On observational methods, besides many of the foregoing works, those of Edmund Selous, W. H. Hudson's *Birds of La Plata*, and others, William Beebe's books and his papers in *Zoologica*; Julian Huxley's notes on the "Courtship of the Great Crested Grebe" in the *Proceedings of the Zoological Society of London* (1914), and on divers in *Spitsbergen Papers* (Vol. I.), may be cited as good models.

Every country in which ornithology is at all active has a scientific journal with which all serious observers should be in touch. In England the *Ibis*, the official organ of the British Ornithologists' Union, has a worldwide scope, while *British Birds* (edited by H. F. Witherby at 326, High Holborn, London, W.C.1) is the nearest approach to a clearing-house for observations. The *Scottish Naturalist*, and the *Irish Naturalists' Journal*, of Belfast, cover the smaller kingdoms; while the *Journal of Ecology* (Oxford) deals with interrelations between fauna and flora from a wide angle. The *Journal für Ornithologie* in Germany, *The Auk*, and *Condor* in America, *Emu* in Australia, *Ardea* in Holland, *Danske Fugle* in Denmark, *Gerfaut* in Belgium, and *Revue Française d'Ornithologie* in France, may be mentioned among the many specialist periodicals all over the world.

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INSECTS

AN INTRODUCTION TO ENTOMOLOGY

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PREFACE

THERE have recently been quite a number of "elementary" books upon insects, and most of them follow a definite system. First there is a chapter upon Structure and Classification, and this is followed by a series of chapters in which interesting life-histories and habits are outlined. Usually, at the end, there is a chapter upon the relationships of insects and man.

I suppose all these books have many readers, but they mostly fail to show any connection between the different parts of the subject, so that the student fails to understand how intimately the three parts, structure, habit, and relationship to man, are associated, and how a thorough grounding in apparently irrelevant branches is absolutely essential for the individual who hopes to become an Economic Entomologist.

In this little volume, one part of my task has been to attempt to bridge these gaps, so that the general reader may know what the training of an entomologist means, and that this training is no more than enough to equip him for his work. I am greatly indebted to Miss K. E. Burnand for her assistance in the work of building up this book.

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INSECTS

CHAPTER I

ENTOMOLOGY IN RELATION TO THE AFFAIRS OF MAN

WE have become so used to regarding ourselves as the "Lords of Creation," that we regard all other living things in the terms of their relationship towards us—they are either useful or harmful or of no importance, and unless we definitely know that a particular insect is of use to us we tend to destroy it in case it might be injurious. On the whole, I suppose this is a sound policy because, although the habits of the majority of insects are still unknown, the habits of those we do know appear to be mostly injurious to us in one way or another. But insects may be useful to us in many ways which are not too obvious at first sight.

We regard bees as useful, and most people, if asked why, would reply that they give us honey. Yet bees are much more useful to us as flower pollinators, especially since honey is no longer the important food material that it used to be before the development of sugar. We recognise the utility of the silkworm because it provides for us a useful fibre, and, although silkworms might provide us with a dainty dish, they are apparently of no other value to us. Both silk-

worms and bees have been so long cultivated by man that the true Silkworm Moth (*Bombyx mori*) is a domestic species occurring nowhere as a wild insect, and the hive bee, although occasionally becoming wild and forming its combs in hollow trees and such places, is only associated with mankind.

We cultivate a few species of bugs because we have found a use for them. For instance, the lac insect, an Indian species of bug, exudes a material which we ultimately put on the market as shellac. The cochineal insect, originally a Central American species, is cultivated because of the red colouring matter which develops in the female, and which we obtain by drying and crushing; but this insect has become of minor importance since the introduction of aniline dyes. We exploit several kinds of gall-producing insects because of the tannin which the plant develops in the galls, and which is of use in the manufacture of ink, and this practically completes the list of insects which we cultivate as being useful to us commercially.

Comparatively recently, however, we have come to recognise that we can exploit various other insects to assist us in the destruction of various species which are injurious to our crops, so that these "parasitic" forms are not only protected and encouraged, but are actually cultivated in various parts of the world and sent out to those parts where insects which they will attack are doing serious damage. We now have such a Parasite Breeding Station at Farnham Royal, Bucks, belonging to the Imperial Bureau of Entomology, for the express purpose of rearing and supplying "para-

sites" of the pests which attack cotton, sugar, etc., in the colonies.

There are, however, vast numbers of useful insects which we do not cultivate, and which many of us do not even recognise as being of any use at all. If one has the courage to turn over a rabbit or a bird, or more courage still, a cow or horse, which has been dead for some time, a loathsome, but at the same time very interesting scene presents itself—hordes of whitish maggots wriggling about in the decaying material, numerous kinds of beetles, mostly black, but many with bands of yellow or orange, and numerous other forms in insect life, all struggling to get out of sight in the mass of decay. Our first instinct is to regard them as disgusting, and yet they are being very useful to us. As soon as an animal dies, putrefying bacteria set to work to break down the organic material, and these release the gasses by which we recognise that putrefaction has set in. If such an animal were placed in an insect-proof cage the bacteria alone would, in time, reduce it to a dry odourless carcass, but the insects, warned of the presence of the corpse by their sense of smell, assemble from all quarters and feed upon the decaying material, so that it is much more quickly reduced to an innocuous condition.

Again, numerous insects inhabit the dung of animals, and here again we have useful insects. Animals feed upon organic material, and once this has been taken into the alimentary canal the digestive fluids act upon it, causing various chemical

changes, and the walls of the gut absorb those materials which are nutritive. The remainder are voided and, being organic material, are attacked by bacteria and insects, etc. These living things feed upon it, and it again undergoes digestion, absorption, and excretion, the excreted materials, however, being much less complex than previously, so that successive layers of animal or plant life break down the organic materials, which are ultimately reduced to such a simple condition that the general vegetation can make use of them as food material. It sounds unpleasant, but, after all, the whole process of life is merely building up and breaking down repeated again and again, and there are just the same materials in the world to-day as there were when life first appeared upon it. The dung-feeding insects, by increasing the rapidity of the breaking-down process, help to make the materials once again available for absorption by plants which are the food of many animals. I have spoken of bees as of importance in the pollination of flowers, the transference of pollen from the stamens of one flower to the pistil of another, but it is not only the hive bees which are thus useful; the bees as a group—and there are vast numbers of species—are by far the most important flower pollinators. Next to them come the flies, many of which, like the bees, seek the flowers for the sake of the nectar and become covered with the sticky pollen which they transport to other flowers. Many flies are scavengers, feeding upon decaying organic matter, so that flies, as a group, are useful, and even the house-fly and blue-bottle belong to this group

of scavengers. Butterflies and moths are also flower pollinators of about equal importance to the flies.

In August and September we suffer inconvenience and some damage from wasps which infest our houses in search of sweet food materials and which damage fruit upon the trees in the garden, and yet wasps are most useful insects. They feed their young upon insects, and one can easily watch them during the earlier part of the year hunting amongst the herbage on the banks and seizing small caterpillars or other insects which are then partially chewed up, to stop their struggles, before being carried off to the nest.

Therefore, with regard to many of these insects we find that they play two rôles; they are useful to us in one way and injurious to us in another. The wasp can scarcely be described as injurious except in connection with the damage it does to fruit on the trees, and its depredations in this direction seem to be increasing. I seem to remember a time when only ripe plums and pears were attacked, and even then it was suggested that fingers or a bruise caused the first damage, but now unripe fruit is readily attacked, even where the skin is perfectly sound. We might, therefore, place the wasp upon the suspect list, as the question will soon arise as to whether its utility as a destroyer of insects is not out-balanced by the damage it does in our gardens.

With regard to house-flies, on the other hand, we can safely say that they are more injurious than useful, though this is due to the fact that we expose our food materials instead of keeping them under fly-proof

conditions. Decaying organic matter contains bacteria, some of which can thrive inside us and cause disease. Some of the material containing them adheres to the hairs of the fly, and germs are sucked up by the insect, whose digestive fluids do not destroy them. Now, the house-fly has very catholic tastes: it feeds readily upon decaying organic materials, and it also enjoys the foods we prepare for ourselves. Moreover, it seems to enjoy feeding to such an extent that even though it has just fed to repletion, it will readily start again if a new supply of food is forthcoming. In order to make room for a further feast, it vomits up the contents of its crop. If, therefore, having fed upon the dung-hill, it comes into the house and discovers the milk or the butter exposed, it disgorges the contents of its crop on the side of the jug, or upon the butter, and feeds again. The vomit may contain disease-producing bacteria, so that, in drinking the milk or eating the butter, we become infected. The fly may also, in cleaning itself by rubbing its legs over its body and wings, deposit bacteria upon our food materials, and bacteria may also be voided with the excreta. It has been shown that the living typhoid bacillus may be passed out of the fly's body a month after the fly has absorbed it with its food.

So far I have spoken of useful insects, some of which also injuriously affect us, but there are a number of insects which, as Lords of Creation, we might describe as having no justification for their existence, as they appear to be merely injurious to us. In many parts of the world the human body-louse is

regarded by the uninitiated as a mere domestic animal, and it is not so long since the women of country districts in Britain looked upon the presence of lice as evidence of fecundity in themselves. As recently as 1919 (9)* 20 per cent. of the Board School children of Britain were lousy. Civilised people are gradually coming to regard lice as unpleasant creatures, but there is no evidence that lice, as such, do any harm to us. Unfortunately, however, they transmit diseases from one person to another, and amongst these is the dreaded typhus, which can only break out in any district where lice or bed-bug are prevalent. The insects suck up the germs of the disease in the blood of a patient suffering from it, and, on passing to another individual, they void some of the germs with their fæces. The puncture made by lice or bed-bugs becomes itchy, and the scratching to relieve this rubs in the fæces and with them the disease germs, and thus, typhus passes from person to person. During the war it was shown that trench fever and an intermittent fever were also transmitted from individual to individual through the agency of lice. -

The mosquito, like the louse, is a perfectly harmless insect in itself. The female sucks blood because blood is an important food for, and aids in the development of, the eggs, although it has recently been shown that blood is not essential, as it was at one time thought to be. Unfortunately, however, the mosquito's manner of feeding is exploited by the

* The numbers in brackets refer to the bibliography on p. 78.

germs of malaria. When the mosquito drives its mouth-parts into our blood capillaries it pumps in salivary fluid, the function of which is to prevent the coagulation of the blood, and probably also to act as an external digestive. If the mosquito sucks the blood of a malarial patient it takes up some of the germs of the disease, and, if these happen to be in the right stage, they continue their development in the mosquito, passing through the walls of the gut, and, ultimately, after about eleven days, they reach the salivary glands. During all this time, the mosquito can continue to feed upon people without causing them any damage other than the irritation at the puncture, but once the malarial germ has reached the stage in the salivary glands, the mosquito, in pumping out saliva during feeding, pumps out the germs also, and thus infects the blood of another individual. Here again, then, another person is the cause of our getting the disease, the insect being the vector or carrier from one to the other; but whereas in the case of the house-fly the insect was of no importance to the disease germ except as a carrier, in the case of the mosquito the insect is a necessary host for the disease germ to enable it to complete its life cycle.

These, then, are examples of insects harmless in themselves which unfortunately transmit disease germs between man and man, and there are a large number of this type, but there are also diseases directly due to the attacks of insects. The common flea is only dangerous as a carrier of the germs of plague, but the "Jigger" or Chigoe flea burrows into the

flesh, which may suppurate and cause bad wounds. Otherwise most of the directly injurious insects are flies, and where fly maggots invade the human body, medical men speak of Myiasis. It is a curious fact that, although fly maggots breathe air like other insects, some of them survive for long periods inside the animal body. In some cases, as for instance where the fly lays its eggs in the nostrils or in an open wound, the maggots may retain contact with the outside air, but in cases where the alimentary canal is invaded, as sometimes happens, it is difficult to understand how the insects obtain the necessary oxygen. Excepting the "Jigger," there seem to be few insects which burrow directly through the human skin, but there is one fly, known as *Dermatobia*, which adopts special means of getting its larvæ into the body. For a long time no one could discover how the larvæ of *Dermatobia* got into the body, and various suggestions were made. One of these was that the fly laid its eggs upon washing hung out to dry, and the eggs on the underclothes hatched when in contact with the body and the larvæ then bored their way in. Now it is known that the *Dermatobia* lays a neat little parcel of eggs upon the underside of the abdomen of a small blood-sucking mosquito, *Janthinosoma*, and that while this mosquito is sucking human blood, having pierced the skin by means of its mouth-parts, the *Dermatobia* eggs hatch, and the larvæ make for the puncture caused by the mosquito and thus enter through the skin.

Domestic animals suffer from insects in the same

ways as human beings—that is, in some cases the insect is merely a carrier of disease germs, while in others the insect itself is the cause of the trouble. Our cattle in Britain suffer from the attacks of the Warble fly (*Hypoderma*), which lays its eggs amongst the hairs, usually upon the legs. The maggots hatch out and themselves penetrate the skin and move through the body until they reach the back, by which time they are getting fairly large. Here they break through the skin and bring their spiracles or breathing pores to the opening, and these wounds may suppurate and cause considerable suffering to the animal. Apart from this, however, the damage done to the skin is such that the value of the hide is greatly reduced and the annual loss in value in our islands runs into some millions of pounds. The bot-fly of the horse (*Gastrophilus*) lays its eggs, like the *Hypoderma*, on the hairs, but in this case the horse licks itself and, if its tongue comes into contact with the eggs, these hatch and the maggots stick to the tongue and thus pass into the mouth. They reach the stomach, where they hold on to the walls by means of their mouth-hooks, and there they feed. Now, there is not a ready supply of air in the horse's stomach, all there is being in the form of bubbles swallowed by the horse while feeding. These maggots are, therefore, specially adapted to these conditions as they possess masses of cells containing hæmoglobin, the red colouring matter of human blood, which has a great affinity for oxygen. The bubbles of gas in the horse's stomach are caught in a vestibule at the posterior end of the fly larva, and

the oxygen is extracted from the bubbles by means of the hæmoglobin. The full-grown larvæ let go their hold on the walls of the stomach and are passed out with the excreta, and shortly afterwards they hatch out as flies. The horse naturally gets on better without these internal parasites, which, if numerous, may cause serious trouble and even death.

These are examples of the numerous insects which injuriously affect us by damaging our domestic animals, but we are also very seriously affected by many species of vegetarian insects, which attack our crops and levy a very heavy toll upon us; in fact, there are few commercial undertakings connected with plants where we do not suffer heavy losses from insect damage. In the tropics, almost all woodwork used in the construction of houses is liable to attack from termites, or so-called "White Ants." These insects shun the light, and under normal conditions are not seen in a house, the first warning of their presence being when a chair or table collapses or when one puts one's finger through a rafter or a door-post. The exposed surface is left intact and the inner parts are eaten away. Again, there are many wood-boring beetles which do considerable damage to lumber in the yards, and after it has been used in the construction of buildings and very many of our older English churches, with their beautiful oak work, are having to be repaired at the present time because of the damage done by a wood-boring beetle. Soft woods are attacked by other species, and many of us have, perhaps, suffered from the collapse of a wicker-chair.

owing to the work of a small beetle in the willow wands.

As Lords of Creation we may ask, What is the use of these wood-eating insects? I have even been told by a pious lady that they have been sent into the world to humble us. As a fact, these insects are useful insects, and, if we may continue in the strain of the pious lady, they have been sent into the world to break down wood-fibre when the plant is either sickly or actually dead. In other words, these insects are scavengers, like the dung and the carrion-feeders. Unfortunately, we kill the trees for our own uses, and, so far, we have discovered no means by which we can teach these useful insects to discriminate between dead wood lying in the forest and wood we are making use of.

If we are going to justify the insects which cause us millions of pounds' worth of damage by destroying our timber, we might put forward a good case for any other insect which we regard as injurious. So far as the world is concerned we might regard the disease carriers as useful in that they reduce the numbers of human beings, and thus postpone the day when birth control will be a *sine qua non*. The insects which attack our crops are really attempting to assist Nature by keeping down excessive numbers of individuals of a particular species. But in adopting this attitude we have ceased to be Lords of Creation, and have adopted what might be the views of the Almighty. Self-preservation being strong within us, we shall continue to take the line that we must adopt all measures to

"protect ourselves," which means that we must endeavour to destroy all those insects which interfere with our own schemes. If this is the wrong view to take, then there is little doubt that before very long insects will dominate us. The mosquito has, according to the views of well-known authorities, retarded civilisation, and even destroyed it more than once. The ancient civilisation of Greece was probably destroyed by malaria, and wave after wave of civilisation in Africa has been dissipated by the same dread disease (3). Now we are learning how to control the mosquito, and many parts of the world which were uninhabitable a few decades ago, are now at least tolerably healthy. We are learning now to overcome some of the insects which attack our crops, and we shall, no doubt, gradually reduce the losses. Everyone at once recognises that the reduction of disease is a good thing; but many people may say: So long as we can grow enough of a crop to supply us, what does it matter if insects destroy the rest? If we have to grow twice as much of any crop as we actually require because insects destroy half of it, it means double the labour in cropping and it means double the expense. Someone has to pay for this, and the losses are mostly passed on to the consumer, the ultimate buyer of the prepared product. If, therefore, we can reduce the losses, the price to the consumer will come down, but as we are now straying into questions of political economy, we can leave this subject, although some of the points raised in this chapter will be expanded as we proceed.

CHAPTER II

*THE STUDY OF STRUCTURE AND
FUNCTION*

It is a common saying that every organism is adapted to its environment, which means that the structure and habits of every animal and plant are such as to fit it to occupy the place in which it lives, the place it lives in being its environment. But this environment is highly complex; it is made up of the climatic conditions, amount of sunshine, rainfall, range of temperature, and so on; the edaphic conditions or nature of, and moisture content of, the soil, and the organic conditions—that is, the living animals and plants occupying the same place. Consequently every species not only has to be able to withstand the extremes of climatic and soil conditions, but has also to hold its own, obtain its food supplies, and reproduce its kind amongst all the other living things, many of which are directly competing with it for food and place, and all of which are in some way affecting it directly or indirectly.

To take a broad example: We can group the animals living in any area into carnivorous or flesh-eaters and herbivorous or plant-eaters. The latter depend upon the vegetation for their food, while the former depend upon the vegetarians. The plants are kept in check because they are eaten, but they are protected from extinction because the carnivorous animals are keep-

ing in check the vegetarians, and thus there is a balance between the three groups. If anything happens to cause a decrease in the vegetation, both groups of animals are affected. If the vegetarians decrease, the vegetation increases and the carnivores are reduced by partial starvation. Of course the inter-relationships are much more complex than the above example indicates, but it is often possible to pick out of the general tangle a series of relationships which has been called a biological chain. Darwin gave an excellent example of such a chain in the *Origin of Species* (7).

Leaving out the intermediate links in the chain, it may be said that the amount of clover seed in any district depends upon the number of cats, which sounds ridiculous. Clover is pollinated by humble bees. "The number of humble bees in any district depends in a great measure on the number of field mice, which destroy their combs and nests. . . . Now the number of mice is largely dependent, as everyone knows, on the number of cats. . . . Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in the district." This chain has since been increased by the addition of another link, as it has been pointed out that old maids, more frequently than other people, keep cats, so that it may be said that the amount of clover seed in any district depends upon the number of old maids.

It is obvious that everything which affects any one

of the links in such a chain affects the whole chain, and, as such a chain is entangled with other chains in the same locality, Nature strikes a balance between all the living organisms, by which, unless something out of the way occurs to upset it, the numbers of individuals of each species remain more or less constant or wax and wane very slowly. But various things do upset the balance. Excessive rain may flood a district and destroy most of the living things, or a hurricane may lay out large areas of woodland, making the district quite unsuitable for the animals which previously lived in the shade of the trees, but more suitable for other forms which will then invade the area and replace the original occupiers.

Man is perpetually interfering with the balance of Nature. He drains marshes and irrigates dry land. He cuts down forests and thereby not only affects the shade-loving animals and plants which sheltered beneath the trees but also affects the climatic conditions, since forest areas are always more moist than open ground and enjoy additional rainfall. In Nature, vegetation is mixed, so that large areas of one species of plant to the exclusion of all others are uncommon. Man deliberately plants large areas of pure forest or of other commercial plants, and all his arboricultural and agricultural methods are at variance with natural conditions. ●

Nature is perpetually attempting to balance. Thus we see that clearings in tropical forests grow up again unless man continues to keep them clear. According to the amount of man's interference the balance may

be quickly restored, so that after a short time nothing remains to indicate the temporary disturbance, or, as is more usual, the balance is restored after a time, but the environment is permanently changed.

The mongoose was introduced into Jamaica to keep down the rats which, originally introduced from ships, were in excessive numbers in the sugar-cane fields. The mongoose reduced the rats in the fields, partly by destroying them and partly by causing them to migrate to the houses. This led the mongoose to look elsewhere for its food supplies, and it attacked the snakes, lizards, and any birds it could catch. But, with the reduction of the reptiles and birds, the insects, which had been kept down by them, began to increase in numbers, as did also the ticks, which became very abundant. Apparently, however, the increase in the ticks adversely affected the mongoose, which consequently became less abundant, and once more lizards and birds began to increase and the balance of Nature was restored, not in its original form, but adjusted to include the mongoose.

The mongoose was also introduced into St Lucia with the object of reducing the rats, and there also the consequences were similar. A mole-cricket (*Scapteriscus didactylus*), which feeds on the roots of various plants, became especially abundant because of the reduction or extermination of a ground lizard, and efforts have been made to re-establish this useful reptile with a view to reducing the ravages of the mole-cricket.

There are certain flies, usually known as blow-flies,

whose primary object in life is to act as scavengers. They lay their eggs in decaying organic matter and their larvæ or maggots eat up the material. Some of these flies lay their eggs in the soiled wool of sheep, especially round the anus, and the maggots have developed the habit of destroying the wool and even eating into the flesh of the sheep and setting up blood poisoning. Large losses result to the farmers every year in the British Islands and other countries from what are called "Sheep Maggot Flies," and, although it sounds absurd, the introduction of rabbits into Australia caused a tremendous increase in "blown wool" in that country. The rabbit was not a native of Australia, but the early settlers had some sent out from the home country. The rabbit found that Australia was the country for which it had always been looking, and it increased and multiplied to such an extent that, in a very short time, it became a serious pest, eating up everything which the settlers planted. Urgent requests were then sent home for something to control it, and a number of weasels and stoats, chiefly collected in East Anglia, were sent out. These animals apparently were unable to cope with the situation, but their removal from this country seems to have been followed by a temporary increase in the number of rats.

As they failed to do the work for which they were transported, other measures had to be adopted and a price was set upon the head of the rabbit. This resulted in vast numbers being killed, and their dead bodies were allowed to lie and decay. The scavenging

blow-flies came to assist in the work of disintegration, and, owing to the abundance of food material, they increased and multiplied to an enormous extent. The rabbits were gradually reduced in numbers and the blow-flies found themselves out of work, and whereas previously only two species had interfered with sheep, now another six have developed the habit and the losses to Australian farmers are very serious. From this last example we see, that, although the blow-flies were originally scavengers, they re-adapted themselves under the stress of circumstances, and this leads us to consider the meaning of adaptation. We have already seen that an organism is adapted to its environment, and, since the environment is constantly varying, any particular species must either be sufficiently plastic to withstand the variations or it will be eliminated by natural selection. Plasticity naturally varies with different species, and many are quite obviously very plastic. For instance, many insects are polyphagous—that is, are capable of eating a number of different kinds of plants and can actually be found on the different plants. They can be transferred from one kind of plant to another, and will continue to feed without any difficulty.

On the other hand, there are many insects which apparently are monophagous, always being found upon one kind of plant. To all appearance, therefore, these species are non-plastic, so far as food is concerned, but, under stress of circumstances, it is found that they can thrive perfectly well upon some quite different food plant. In Montana, U.S.A., in 1909 certain owners

decided upon cleaning up their orchards, and in so doing they destroyed quantities of a common weed, *Artemisia tridentata*. This was the normal food plant of a beetle, *Cercopaeus artemisiae*, which, in the absence of the *Artemisia*, attacked the cherry-trees and did considerable damage. In the vineyards in a certain district in France it was discovered that the advent of a small bug (*Nysius senecionis*) on the vines coincided with the ploughing in of a weed pest (*Diplotaxis eruröides*), which is its normal food plant and which it definitely preferred to the vines.

Cameron (5), in 1914, showed that a small fly, the Belladonna Leafminer (*Pegomyia hyoscyami*), attacks henbane (*Hyoscyamus niger*), but, in the absence of this food plant, belladonna (*Atropa belladonna*) is readily eaten. The caterpillars of the Nun Moth (*Eymantia monacha*) feed upon spruce leaves on the Continent and often do such damage by defoliation that the trees are killed, unless active measures are taken to destroy the pests. In Britain, the caterpillars are mostly found upon oak, birch, and such trees, and do but little damage to conifers.

These latter, then, are examples of what we might call "potential plasticity," which only becomes evident under certain conditions, and there are other examples where, so far as we can see, the plasticity exists but is never used at all. For instance, besides the wasps, which live a social life, there are a number of solitary forms in which each female lays up a store of food in a series or group of cells, laying one egg in each cell. The food is for the wasp grub which hatches from

the egg, and the mother stores up sufficient to enable the grub to grow to full size and to change into a pupa. Each species of solitary wasp stores up a particular kind of food for its offspring. One will store caterpillars, another bees, another beetles, another beetle larvæ, another spiders, and so on: but the one which stores caterpillars will never change over to flies or anything else. Yet experiment shows that the wasp grub, which normally feeds upon caterpillars, can thrive equally well, say, on beetle larvæ, and yet apparently this plasticity is of no use whatever to the species.

Here is an example of lack of plasticity in feeding powers. There is a solitary wasp (*Sapyga 5-lineata*) which lays its eggs in the cell of the small Blue Osmia Bee (*Osmia cærulescens*). The egg of the parasite hatches out quickly and the wasp grub feeds upon either the egg or the young grub of the Osmia. Having finished this it changes its diet, feeding upon the mass of honey and pollen which the mother bee had laid up as food for its own offspring.

A closely related bee, the Red Osmia (*Osmia rufa*), is seldom attacked by the Sapyga, although from time to time the parasite lays its egg in the cell of this bee. Apparently the only thing which prevents the Sapyga grub from growing up in the Red Osmia cell is that the honey is scarce compared with the pollen, that is, the food material is too dry, because experiment shows that the Sapyga grub can grow up quite well on the Red Osmia food store if a little honey or treacle is mixed with the latter. As we shall see in a later

chapter the adaptation between insects and flowers is sometimes so fine that a species of plant may be entirely dependent upon some particular kind of insect for its pollination, which, of course, means that the plant is limited as to its geographical range by the distribution of the insect.

Animals and plants living in countries where there are extremes of temperature in winter and summer are adapted to these conditions, sometimes by the amount of fat or the thickness of fur in the different seasons and sometimes by going to sleep during the winter (hibernation), or during the summer (æstivation). Such climatic changes are gradual, so that the organism gets time to adapt itself to the change, but some organisms are capable of rapidly adapting themselves to changed conditions. For instance, some estuarine forms withstand equally well salt, brackish, and fresh water.

There is a small beetle (*Octhebius lejolisi*) which occurs in rock pools on the coasts of Western Europe and endures remarkable and rapid changes of environment. After a storm the rock pools are filled with pure sea water. If a spell of calm and dry weather ensues the water is slowly evaporated by the heat of the sun and the salt concentration increases until the pools dry up. Heavy rain will reduce the salinity until the water may become almost fresh. During the middle of the day the temperature of the pools rises very high, while at night the temperature quickly falls. Under these changing conditions the little beetle lays its eggs, and its larvæ grow to maturity.

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The above are just a few random examples of the plasticity of the organism—that is, of its powers to adapt itself to its environment—and now it is time we inquired as to what is meant by the word “Adaptation.” Adaptation is a matter of habit in relation to structure. Sometimes from a study of structure, including form and colouring, we may guess at the habits, but only to a limited extent. We may take it as an axiom that every structure is either of use to the organism possessing it or is the remains of something which has been of use to the ancestors. Knowing that bees visit flowers, it is fairly safe to foretell when a new bee with lengthened mouth-parts is discovered that it searches for nectar chiefly in long tubular flowers. Knowing the ordinary habits of ground beetles, we may guess with some expectation of being right that a flattened species lives either under bark or in some circumstances in which its flatness is of use to it; the real point being that structure, form, or colouring can be of no use to an organism unless the habits are in conformity with it: in other words, habits are adapted to the structure of the organisms. Of course, in many cases, habits are the direct outcome of the structure, but there are other cases in which there is no apparent connection between the one and the other, and yet the structure would be quite useless without the habit. For instance, many insects are so shaped and coloured that they harmonise with their surroundings and are very difficult to see. There are brown caterpillars shaped and marked to resemble twigs, and there are stick and leaf insects which

so closely resemble twigs and foliage that it is almost impossible to discover them. There are moths which look like the bark of trees, and others which look like patches of lichen, and so on. In all these cases, however, the value of the appearance depends entirely upon the insect remaining motionless during the day-time. Sticks or leaves, bits of bark, or of lichen moving about would attract the attention of passing birds and animals, and the cryptic appearance would be quite useless. Consequently, all cryptically-shaped-and-coloured insects, and other animals, are active at night and passive during the day.

If a number of butterflies of different kinds are offered to some young and inexperienced insectivorous bird or animal, it will be found that, for the most part, the brightly-coloured ones will be rejected with obvious signs of dislike while the quietly-coloured ones will be eaten, from which we may draw the obvious conclusion that the brightly-coloured ones are distasteful. If we now have an opportunity of observing some of these butterflies alive and under natural conditions, certain peculiarities of habits will be easily observed. The brightly-coloured ones fly lazily and slowly, are easy to catch in the net, and when they rest they spread out their wings as if to display their gaudy colours. The dull-coloured butterflies have a rapid zigzag flight, are difficult to catch in the net because of their dodgy flight, and when they rest they close their wings vertically over their backs, exposing only the undersides, which are often so coloured as to harmonise with the surroundings. The

brightly-coloured kinds are advertising their presence, and insectivorous birds, having bought their experience by catching a few, pass the others by. The safety of these forms lies in making themselves as conspicuous as possible so that the birds may not mistake them for something dainty. The safety of the palatable forms depends upon their making themselves difficult to catch and difficult to find when at rest, so that the difference in habit between the two types is associated with difference in colouring.

But there are relations of the quietly-coloured butterflies which have taken on the bright colouring of the unpalatable forms, and, just as they have developed the colouring, so also have they developed the habits. They mimic the unpalatable forms in colouring and habit, and are therefore protected because the birds do not distinguish them from their models. But this is not the end of the story.

Their success depends not only upon their colouring and habits, but also upon the fact that they are scarcer than their models, and it is easy to see why. If the young bird, learning by experience what is edible and what is not, finds that a few of the brightly-coloured butterflies are good but that most of them are nasty, it makes up its mind not to waste time on them; but if it happened to find that most of them were good and only a few nasty, it would continue to feed upon them, rejecting now and again the unpleasant ones. Thus the mimic would not only lose the protection it gains by its mimicry, but the model would quickly cease to exist. Here, then, we see a

further very delicate adaptation. The mimic must always be less abundant than the model or it destroys itself.

But what has all this got to do with economic entomology? What is the importance of a knowledge of structure and habit to the man who has only to destroy insect pests? The scattering of Keating's powder, the "swatting" of wasps, or the putting up of fly-papers does not require any previous training, and, to many, these include almost everything which comes under the heading of economic entomology. If an insect is destroying a crop, the layman says, "Kill it." But how? It would be very expensive to go over a field with Keating's or with a swatter. The layman probably says, "Hasn't anybody else had the same trouble, and, if so, what did he do?" Here we have our first scientific problem. If we are going to find out whether someone else has had the same trouble we must be able to identify the insect, and to this end we must examine its structure in order to determine to which group it belongs and where it comes within that group, and we are thus undertaking research in "systematic" entomology. The layman may retort, "Get it named at the Natural History Museum"; but that does not get rid of the fact that the study of systematic entomology is necessary before we can name our insect.

Having discovered the name of the pest, we may be able to find a description of its life-history and habits, if they are known; if not, we must set about studying them. "What for?" says the layman. Be-

cause the insect may lay itself open to attack at some stage, or at some time of the year, or even at some time of the day, and be otherwise difficult to destroy. If, for instance, we discover that a moth lays its eggs in batches which are easy to find, or that the caterpillars readily expose themselves to attack, it is waste of time to try and destroy the scattered moths. Why waste the day trying to destroy beetles upon fruit bushes if a study of the habits reveals the fact that they are much more readily found at night? Thus a careful study of habits provides the decision as to the method to be used for overcoming the pest.

But the layman will probably counter this statement by saying, "Well, by this time the habits of most of the ordinary pests are well known, so that there is no need to spend any more time on that part of the subject." From what has been said earlier in this chapter, it is obvious that the habits of insects often vary from country to country, and even from district to district, and very slight variations may make a great difference as to the method or time of attack. For instance, the eggs may hatch earlier in one part of the country so that the whole life-cycle will be in advance in one place of what it is in another. If the egg stage is the one which is most easily attacked, it may be necessary to operate a week or more earlier in one place than in another; otherwise the work will be a useless waste of time, and, of course, where it is on the large scale, a waste of money also. In connection with this variation from one district to another several papers have been written, notably by

A. D. Hopkins (12, 13, and see 6), of the United States, who has worked out what he calls the "Bioclimatic Law" for an area of his country from which he shows that if an insect normally appears, say, in the adult stage, at a particular date in one district, it will be so much later in another district, and so much later in another. As has already been shown earlier in this chapter, the fact that we know the life-history of a species in any one country is not justification for assuming that it is the same in another country, and we need only remember the different feeding habits of the Nun Moth caterpillar on the Continent of Europe and in Great Britain. The common Slave-making Ant (*Formica sanguinea*) varies its habits in different places. Whereas in one district all the nests will be found to contain numerous slaves, in another the *Sanguinea* makes no slaves, and does all the work itself.

Closely related species frequently differ remarkably in habits, so that a knowledge of the life-history of one is useless as an indication of that of another. The Large White or Cabbage Butterfly (*Pieris brassicae*) lays its dark yellow eggs in batches of twenty or more, and the caterpillars, when they emerge, remain together and continue together until they are full grown. They are conspicuously coloured in black and yellow, and are usually to be found upon the upper side of the leaves of the food plant. The Small White Butterfly (*Pieris rapae*) lays its pale yellow eggs singly, and its caterpillars, which are of the same green colour as the food plant, are solitary, and spend the daytime lying motionless, usually on the underside of the

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leaves. A small bug, known as the Apple-Sucker (*Psylla mali*), lays its minute yellow eggs round the apple buds in the autumn and the young hatch from them in the following spring. A closely related species, not too easily distinguished, known as the Pear Psylla (*Psylla pyri*) winters in the adult stage, sheltering in crevices in the bark and under rubbish during the cold weather, and lays its eggs in the spring. A method of destroying the Apple Psylla is to paint the twigs with lime or some other chemical wash during the winter and thus to destroy the eggs, a method of treatment which would obviously be useless against the Pear Psylla.

Several species of aphids or "green-fly" attack the apple. One of these, the Green Apple Aphid (*Aphis pomi*), winters in the egg stage on the twigs and round the fruit-spurs. When the leaf buds are opening in the spring these eggs hatch, and the young aphides enter the opening buds and suck the sap of the young leaves. In two or three weeks these individuals have grown into wingless females, which soon produce a brood of young aphides, mostly wingless like their mother, though a few develop wings as they grow. These young are full grown in another two or three weeks, and they disperse about the tree, the winged individuals flying to other apple-trees in the neighbourhood. These again give rise to another generation, and this goes on all through the summer, six or eight broods being produced by early autumn. At this period males appear for the first time, and mate with special females, these latter seeking out apple twigs,

and each laying from two to six eggs, thus completing the annual cycle, the eggs lying dormant through the winter.

It would seem logical to say, "now we know the life-history of this aphid, that of any other aphid, especially on the apple, should be much the same"; but a study of other species shows that this is not the case. The Rosy Apple Aphid (*Aphis sorbi*) commences active life in the spring in the same way as the other and, until about June, its habits are similar, but at that time winged females appear and fly away, and in a very short time every individual has disappeared from the apple. For a long time it was not known what happened to these winged individuals, but it was ultimately discovered that they fly to a small weed known as plantain or rib-grass, and there continue the life-cycle of the species. In the autumn winged females are again produced, and these return to the apple, where they give birth to females and males, the former laying the eggs which lie dormant through the winter.

The Woolly Aphid, or, as it is sometimes called, "American blight" (*Eriosoma lanigera*), like the Rosy Apple Aphid, normally relies upon two host plants, the apple and the elm, for the completion of its life-cycle, but in the autumn it gives rise to a generation which goes down to the roots of the apple and there survives; individuals coming up to the trunk and twigs in the spring and re-establishing the attack on the subærial parts of the tree. Thus they intensify the infestation which would otherwise depend only

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upon the arrival of winged individuals from the elm about June, or, rarely, upon winter eggs laid in the cracks of the bark of the apple.

Here, then, are three apple species of "green-fly," and it is quite clear that a minute knowledge of the life-history of one of them is of little use in devising methods of attacking either of the others. Perhaps enough has been said in this chapter to convince the layman of the intimate connection between a knowledge of the structure and habits of insects and the destruction of insect pests, or, in other words, that the successful carrying out of this work depends upon that knowledge.

Governments and laymen in this country have been slow to realise that the successful application of science requires a fundamental knowledge of that science. But we have now become wiser, and our Committee of Scientific and Industrial Research and other committees and corporations provide funds for carrying out researches in pure science, regardless of whether or not the ultimate object of the work is economic, on the principle that sooner or later such work will directly or indirectly become useful. More recently the Empire Marketing Board has come into existence, and it has been quick to show by its wise distribution of the funds provided for it that it recognises the importance of the study of pure science in the successful exploitation of the agricultural products of the British Empire.

CHAPTER III

INSECT PARASITES AND PREDATORS

THE term "parasite" literally means one who takes food with another, and we might, therefore, justifiably so describe the friend whom we have asked to lunch. So far as insects are concerned, there are very few such parasites, and most of these occur in the wasp and bee families, where the solitary wasps and bees construct cells, lay their eggs in them, and store them with food for their future offspring. The parasite members of these families lay their eggs in these cells and the parasite grub eats up part or all of the food stored in the cell and, sooner or later, the egg or the developing grub of the host. But the term is used in a much wider sense. There are so-called ecto-parasites and endo-parasites, which live and grow upon the outside or within their host, and if we restricted the name "parasite" to these we might define an insect parasite as one which passes at least part of its early life upon or within an animal (as opposed to a plant) host, to the serious detriment of that host.

The definition would include all the highly specialised insect parasites other than those already mentioned, which might be described as predators, and all such highly specialised parasites are confined to three of the main groups or Orders of insects, the Beetles, the Flies, and the Bees and Wasps. But various insects with very different habits are described as

parasites. Lice spend the whole of their lives associated with warm-blooded animals, not only for the sake of the blood which they suck, but also for the sake of the warmth. They would almost come within our definition, except for the fact that they do not destroy or seriously injure their hosts. Fleas are in a different category. They only occur on animals in their adult stage, their eggs and larvæ being found in dust and other débris such as occurs in empty houses, chicken-runs, and such places. If fleas are parasites, then mosquitoes and other blood-sucking flies are also parasites, since their relations to their hosts are similar. The Bird- or Biting-Lice (*Mallophaga*) are described as parasites, and yet they only feed upon the débris of feathers and fur and flakes from the skin of birds and other animals, so that they are really scavengers. It is quite clear that a definition to include all these insects of very different habits will be a very broad one. If we define as a parasite an insect which lives at the expense of its host, then every predaceous insect comes within the category, and it is rather interesting to note that in the various "Parasite-breeding" Stations, in different countries, a large part of the work consists in breeding certain types of predators. These are insects which are restricted in their diet to a limited number of types, and in order to distinguish them from insects which will eat numerous other types of insect food, they are known as "special predators" as opposed to "general predators."

For the purpose of this chapter, therefore, we will confine our attention to those insects which come

within our limited definition, which includes ecto- and endo-parasites, and also to these special predators, our definition of the latter, as given a few lines above, being such as will include the bee and wasp parasites mentioned in the first paragraph of this chapter. And first with regard to parasitism. It is quite certain that it has arisen independently in the three large groups in which it occurs, and there is little doubt but that it has arisen more than once within a group. Moreover, it has probably originated in several different ways. If we examine the parasitic or cuckoo-bees, we find the curious fact that most of them bear some resemblance to the species which they impose upon. The hard-working female solitary bee, having selected a site for her cell or cells, commences work by bringing in material, it may be pellets of earth or clay, as in some species, or chewed-up plant tissue as in others, and gradually builds up a wall. The bee then becomes a forager, gathering nectar from flowers and converting it into honey in her crop, and pollen which adheres to her body. She brings this material back to the cell, disgorges her honey, and unloads her pollen, mixing up the two to form a paste. A number of journeys, it may be ten or fifteen, are required in order to complete the store of food material in one cell and, this having been done, the bee then lays an egg upon the pollen paste. Then once more she becomes a builder and closes up the cell. The cuckoo-bee, always searching about for her host, discovers a cell during its preparation and waits her time until either the foraging is completed or the egg has been laid and, selecting a

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time when the owner of the cell is out, she slips in and rapidly deposits a single egg on the floor near the pollen paste. The host bee returns and either does not recognise the presence of the strange egg or does not realise its significance and, when she completes the closing of her cell, the two eggs, her own and that of the parasite, are left with a supply of food sufficient only for one. The parasitic egg usually hatches first and the young grub either commences to feed upon the pollen paste or at once attacks the egg of the host; at any rate the cell is ultimately emptied of its food and only one grub, that of the parasite, survives to pupate.

Now the first thought upon this matter of parasitism is that the parasite saves itself the trouble of building and stocking cells for itself by laying its eggs in the cells of other bees, and we may take it that this kind of parasitism actually arose through individuals getting this labour-saving idea. Each species of solitary bee builds its own type of cell and stores it with its own type of pollen paste, the latter being sometimes very moist because it consists of much honey in proportion to the pollen and sometimes very dry when the pollen is in excess. If an individual bee gets the idea of saving itself trouble it would seem natural that, for the sake of the welfare of its offspring, it would lay its egg in a sister's cell rather than in that of a strange species. Moreover, it would perhaps understand the habits of its sisters and would instinctively know, as they know, the different stages in the process.

That this was probably the origin of the cuckoo-

bees is rather borne out by the fact mentioned earlier that many of them somewhat closely resemble their hosts in appearance. We may take it that this type of parasitism has been a paying proposition, and that many individuals in a species have followed the fashion until the idea has become so popular that there have not been left enough working sisters to use as hosts. This has led the parasites to attack another species, probably a closely related one, and the evolution has been so comparatively recent that many of the species of cuckoo-bee are still at work upon their near relations; hence the resemblance in appearance. There are actually some species with regard to which it is not yet certain whether or not they are parasitic, and it is possible that these are species in which parasitism has only just commenced; in which case, of course, evidence by different observers is likely to be conflicting (20).

But although these are called "Parasitic or Cuckoo-bees," there is a great group of forms in the Bee and Wasp Order, or Hymenoptera, known as the *Hymenoptera Parasitica*, in which the majority of the forms are ecto- or endo-parasites, and they have developed parasitism into a fine art. If the origin in this group was due to laziness, the parasites seem to have got to love their profession and have spared no pains to elaborate it. Although the majority of this group are parasites, included with them is a family known as *Cynipidae* or Gall-flies, which would be better called "Gall-wasps," as there are no gall-producers amongst the true flies.

The Cynipids lay their eggs singly in the tissues of plants and the irritation caused to the plant tissues, either by a secretion produced by the mother at the time she inserts her egg or by the young grub after it emerges from the embedded egg, causes the plant tissues to proliferate into a gall. The same species of gall-wasp always causes the plant tissues to develop into a definite type of gall which can always be associated with that particular gall-wasp. The grub of the gall-wasp becomes embedded in the midst of the gall tissue upon which it feeds and, when it is full grown, it turns into a pupa within the remains of the gall, from which the adult later escapes by biting its way out.

Here, then, we have a type of vegetarian insect which is included within the group of the *Hymenoptera Parasitica* because its structure clearly indicates that it is closely related to the parasitic forms, and it seems reasonable to believe that these latter, now entirely dependent upon insects for their food, have originated from vegetarian ancestors. In the galls of many of these Cynipids there are frequently to be found a number of grubs feeding, like the owner of the gall, upon the proliferated plant tissues. These belong to related species which, like the cuckoo-bees, have developed the habit of saving themselves trouble by laying their eggs in ready-made homes. They are mere guests or "inquilines," and are true parasites in the sense that they share the food with the owner, but otherwise they do it no harm. Besides these guests there are yet other grubs, closely related to

them, which are carnivorous and, instead of feeding upon the gall tissues, feed upon the occupants of those tissues, and it seems reasonable to regard these as having originated from the inquilines by a change of diet. Now these are not parasites according to our definition but are predators, the eggs being laid in proximity to, but not upon, the host species, and the grubs grazing upon the host grubs just as any other predatory insect, far removed from any suggestion of parasitism, feeds upon its prey. And yet it seems possible that these predators formed the intermediate link between those forms which live upon a vegetable diet and the true ecto- and endo-parasites (11). After all, the difference between a predator and a parasite is really very small.

Just as in the case of the solitary bees, the solitary wasps, of which there are a number of families, each containing a number of species, store up in cells food material for their offspring; but whereas the bees store pollen and honey the wasps store insect or spider material, each kind storing a certain definite type of food as already mentioned. The simplest of these solitary wasps, a group known as the "Scoliid wasps," construct no cell, but hunt for the larval food, which consists of the juicy grubs of certain beetles. In order to find these, the mother wasps burrow in the soil, as the white grubs feed upon the roots of plants. Having found such a beetle grub, the mother Scoliid stings it in order to paralyse it and then lays a single egg upon it. This egg ultimately hatches out and the Scoliid grub feeds upon the living beetle larva and

becomes full grown about the time it has exhausted its food supply.

The structure of the Scoliid, when compared with that of other solitary wasps, is more simple and therefore we regard it as a more primitive type. We are justified in believing that insects of more primitive types will have more primitive habits, and we find therefore that these primitive wasps were ecto-parasites and that, as the wasps evolved, they elaborated their parasitism. Instead of merely finding the host and laying an egg upon it, they have developed the habit of constructing a special cell and bringing the host to it. But notice how very near this primitive Scoliid is to a simple predator. If, instead of laying its egg upon the host, it laid it in its neighbourhood, and if the young grub on hatching had to seek for its food, the Scoliid would be a typical predator, so that the difference between a predator and an ecto-parasite is almost negligible. We find amongst the *Hymenoptera Parasitica* quite a number of forms in which the egg is not laid upon the host, the young parasite grub having to find its way, sometimes a very strenuous way, to the food material. In some cases this may be a pre-parasite phase, whereas in others it seems as if it were a modification of the parasite habit.

Having then established the exceedingly close relationship between predator and parasite we can argue that the former gave rise to the latter, because of the number of more primitive predatory insects and the complete absence of true parasites in these more primitive groups. And yet if we compare vegetarian insects

with carnivorous ones we find that the majority lay their eggs upon or in the material which will later form the food supply of the young, so that the development of the carnivorous habit brought with it the necessity of the young insect hunting for its prey, whereas the development of the parasite restored the position in which the mother placed her egg so that the young, when it hatched, could feed at once. We saw in the case of the cuckoo-bees that, according to Wheeler's theory of their origin, they were destroying their hosts, but, from an economic point of view, this is a bad policy, and as a fact the average parasite does not work upon this principle. It usually avoids committing suicide, either by having more than one host, so that if one fails there is some other to rely upon, or else its abundance is such that it does not seriously affect the abundance of its host. The former type of parasite is described as polyphagous as opposed to the latter which is monophagous, and we may regard this latter as more modern because it means a higher degree of specialisation and adaptation between parasite and host. And the relationship is such that if the host becomes more abundant the parasite also increases in numbers, and when the host numbers diminish, the parasite numbers do the same.

If we determine from year to year the abundance of the host, we can trace out a curve showing how the species waxes and wanes, and a curve drawn to show the history of the parasite will be found to show the same form, but the maxima and minima will always be later than those of the host. That is, the host

reaches a maximum abundance and begins to decrease, and not until the host has passed its maximum does the parasite reach the apex of its curve. We can deduce from this, that, but for the parasite, the host would be more abundant, or, in other words, the parasite is the factor, or one of the factors, which controls the abundance of the host. It was suggested by an American entomologist, Asa Fitch, more than seventy years ago, that use might be made of parasites to assist in the control of insect pests. Nothing, however, seems to have been done at that time, and in 1872 a M. Decaux made the suggestion that the Apple-blossom-Weevil (*Anthonomus pomorum*), which was very troublesome in certain parts of Picardy, might be controlled by conserving its parasite. Not until 1880 was the experiment actually made in an area of about 800 trees which were very badly infested and were somewhat isolated from other orchards.

The mother beetle bites a small hole in the developing blossom and inserts an egg, and the beetle larva feeds upon the pistil and stamens. As a consequence, the petals do not open but the bud remains globular and turns a rusty red. The larva changes to a pupa within the so-called "capped" blossom, and the beetle later hatches out and escapes. The usual method of dealing with this trouble had been to gather the capped blossoms and destroy them. Now the weevil is attacked by a small parasite, and M. Decaux pointed out that the destruction of the capped blossoms meant not only the destruction of the weevils, but also that of the parasites, and he suggested that if the blossoms

were collected and placed in such conditions that the parasites could escape while the beetles could not, it would be a wise course to pursue. Consequently the blossoms were stored in boxes covered with fine wire gauze screens, the mesh being such that the parasites could pass through but the weevils could not, and these boxes were placed in the orchards. As a consequence, it was calculated that a million beetles were destroyed in the first year of the experiment, while about two hundred and fifty thousand parasites were released. The experiment was repeated in the following year, with the result that the parasites so reduced the number of weevils that for ten years afterwards the damage done by the pest was inconsiderable. Since that time, in various parts of the world, efforts have been made to destroy the pest by increasing the numbers of the parasite, and in Czecho-Slovakia, for instance, the cocoons of the Nun Moth, which are easily found, are collected and stored so as to permit of the escape of any parasites they may contain without allowing any of the moths to get away.

By such means it is possible to exploit the native parasite and increase its numbers, but, unfortunately, most of the serious pests in the world are insects which have been introduced, usually of course by accident, into the countries where they are interfering with man's activities. Once the possibilities of the parasite were recognised it was suggested that if it could be shown to be the chief controlling factor in the original home of an insect which had become a pest elsewhere, it might be introduced to diminish the

numbers of its host in the country where the latter had become abundant through lack of control.

Now we may refer once more to what was said in the previous chapter about the balance of Nature. The introduction of a new insect into any district tends to upset the balance, and this new insect may or may not be such as to readily fit into the scheme of things. If it does not, it means that there is nothing in the district it has invaded which can keep down its numbers and, as a consequence, it increases and multiplies, seriously interfering with other forms by occupying space and eating up their food. Where it becomes sufficiently abundant and develops a taste for our cultivated vegetation, we recognise the appearance of a new pest. In its native country this pest may well have been a harmless member of the complex of animals and plants and, if so, it was controlled by some agency. It might be that the control was some physical factor, but on the other hand, if the control was a parasite, why not introduce the parasite to control the pest?

The idea seemed plausible to those who first thought of it, and it is perhaps a little unfortunate that one of the earliest experiments in this direction was a most extraordinary success. In California the orange groves were suffering severely from the attacks of an insect known as the "Fluted" or "Cottony-cushion" Scale (*Icerya purchasi*), which sucked the sap and by its sticky excretions gave a hold on the leaves to the spores of a fungus, which assisted in destroying the plants. Investigation showed that the *Icerya* was a

native of Australia, and entomologists were sent there to observe what it was that prevented this scale-insect from being a pest in its native country. It was discovered that a small ladybird beetle (*Novius* [*Vedalia*] *cardinalis*) fed upon the scale and kept down its numbers. Now a large number of the *Coccinellidæ* or Ladybird beetles feed, both in their adult and larval stages, upon scale-insects and upon aphides or greenfly. The beetles lay their eggs in small batches in the neighbourhood of the food material and the young larvæ crawl about and graze upon the abundant prey. They are, therefore, special predators and not parasites in the true sense of the word. After one or two failures, a small batch of the *Novius* reached California, where it was carefully looked after in insectaries, and in a short time a large batch of descendants was available for distribution to the orange groves. From the first the experiment was a success, the beetles and their larvæ destroying the scale until the latter almost disappeared from the district. But it is always necessary to keep up the supply of the beetles by breeding in insectaries, as the insect apparently has not succeeded in establishing itself, and the scale either is never completely exterminated in any district or else it reinvades the district after the disappearance of the beetle. The beetle has to be supplied again when the pest once more becomes abundant. Not only has this beetle been successful in California, but in practically every other country where it has been introduced to deal with the Fluted Scale, and one advantage about it is that it is mono-

phagous—that is, the Fluted Scale is its only food. The success of this experiment led to a number of others of the same kind, the results of which were for the most part disappointing, the reason being that it is impossible to foretell whether an introduced parasite or predator will behave in the same way in the new country as it did in its native home. It is brought into an environment which, but for its host, is completely different from the native environment, and, if it survives at all, it may well change its habits and it may even itself become a pest by reducing the numbers of some useful insect. The failures, as a rule, have been due either to the disappearance of the parasite or to its failing to do the work for which it was introduced.

But although we may describe the introduction of parasites or predators as of problematical value for the control of insect pests, by a very careful study of the life-history and habits of the pest and of its relationships with other species in its new environment it is possible, so long as the complex of species in the affected area is not too great, to introduce a parasite with a reasonable certainty of success. Nowhere has this type of work been done better than in the Sandwich Islands, where, by the most careful study of the fauna and flora, which is naturally limited because of the comparatively small size of the area, the entomologists have been able to introduce parasites to control many different pests and always with either complete, or a very marked measure of, success. From the model work done in Hawaii other islands have had similar

successes, and it may be possible some day to get the same measure of success on the large continents, where of course the interrelationships of living things are much more complex and are in perpetual danger of interference from invasion by species from surrounding areas.

It should be clear from what has been said in this chapter that the exploitation of the parasite and special predator requires first of all a study of the habits of both the pest and the parasite, and a knowledge of structure is involved in the study of the relationship of the one with the other. The fact that the study of the environmental complex of the pest has been shown to give good results, further proves the absolute necessity for a thorough knowledge of the whole subject of entomology on the part of anyone who would desire to be an economic entomologist.

CHAPTER IV

INSECTS AND PLANTS

THE first and most obvious relationship between insects and plants is that in which the former feed upon the latter. We may take it that the vegetarian type arose very early in the history of insects, whatever may have been the primitive type, so that plants have long been exploited, and insects have become adapted to eat every part. While some attack the roots, others

feed upon or within the stem or trunk, while others again devour the foliage, and still others destroy the flowers. We may also take it that, in the majority of cases, the protoplasm and sap of the plant are what are sought after, but it is interesting to notice that in most cases the wood-borers occur chiefly in trees which are either deteriorating through age or disease, or in fallen and cut timber where the flow of sap has ceased. In the case of the Bark-beetles (*Scolytidæ*), for instance, we describe them mostly as secondary pests, since they do not usually attack trees with a full circulation of sap, and yet some of the secondary pests may become primary and attack healthy trees under certain conditions. It has been shown that very many of these wood-eating insects are quite unable to digest the wood for themselves, but that they contain within them micro-organisms, which convert the lignin into a material digestible by the insect. An interesting example of "Symbiosis" or mutual advantage to both organisms (4).

In connection with the statement just made that the wood-borers attack trees past their best, it is interesting to notice that observations on insect pests in most parts of the world have shown that usually the plants which suffer most are the weakly ones, and we shall return to this subject later on in this chapter.

It seems probable that the earliest vegetarian insects fed upon vegetation in general, and were therefore polyphagous. Specialisation or fine adaptation usually means limitation, and therefore we assume that the monophagous insect—that is the insect which only

has one food plant—has evolved from the polyphagous and has gradually become adapted in its method of feeding, and of dealing with the food internally, to the peculiarities of that particular food plant. But monophagy, so far as vegetarian insects are concerned, has not yet developed to any great extent, and, although no insect is capable of eating every kind of vegetation, the majority have a list of at least several possibilities. In some cases we find a particular species indifferently dispersed over several species of plants, while in others we find that an insect definitely prefers one type of food and only takes to another in the absence of the first as mentioned in Chapter II. (pp. 25, 26).

The Gipsy Moth (*Lymantria dispar*) was accidentally introduced into the New England States of North America in 1868 or 1869. It took from twelve to twenty years to establish itself sufficiently to become a serious pest, and by that time the caterpillars were in millions, stripping the leafage of the woods, fields, and gardens so that in midsummer, over large areas of ground, the vegetation was almost devoid of leaves. Very few trees were immune, so that the range of food of the caterpillars was a very large one. At that time the species showed great vigour, and each female moth laid on an average 500 or 600 eggs. As time went on the fecundity decreased, and, with this loss of vigour, there developed a selective taste on the part of the caterpillars, so that now many trees are immune from attack which formerly were readily eaten. By 1913 it was described as "no longer prominent as

a field or garden pest"(10). And in this short history of the gipsy moth in America we seem to have an epitome of the evolution of the feeding habits of insects. So long as an insect is more or less omnivorous the food is perpetually liable to be changed from generation to generation, but, as soon as a selective taste develops, the spreading out of a species into new areas may cause different strains to develop. Various experiments which have been made indicate that physiological changes do occur so that individuals of the same species divide up into groups; one group confining itself to one type of food plant, while another group concentrates upon another type.

In the case of the belladonna leaf miner fly, already referred to in Chapter II. (p. 26), its normal food plant is henbane, but, in the absence of henbane, belladonna is readily eaten. But Cameron found that it would also eat beet and mangold, and that adult flies reared from larvæ which had been fed upon belladonna would not lay eggs upon mangold and that females reared from larvæ fed upon mangold would not oviposit upon belladonna. He suggested, therefore, that, "within the limits of a single polyphagous species, certain well-defined "biologic" species may be established, each of which shows a marked tendency towards one of their food plants. At the same time, Davidson, working with an aphid (*A. rumicis*)—well known to people who grow broad-beans, as it appears upon them in its black swarms about June—found that it had two life-cycles, one of which passes from the winter host, dock (*Rumex*), to the summer

host, broad-beans, and thence back to dock, while the other spends the winter upon spindle-tree (*Euonymus*), and passes to poppy and also to mangolds and beets, etc., in the summer. He suggested that "if these two parallel life-histories were stable, the question of the influence of the host plants on aphids is an important factor. The two life-cycles seemed to show that the preceding host plant upon which a generation of aphids is produced, has a determining influence on the species of plant subsequently selected by the winged migrants" (8).

In the previous chapter reference was made to the habits of the Woolly Aphis (*Eriosoma lanigera*), and to the fact that rarely the sexual forms appeared upon the apple. Now it is clear that in such a case the life-cycle contains a number of generations of parthenogenetic females on the apple and a few generations, including the sexual ones, upon the elm, and that the apple generations can get on either by continuing during the winter upon the roots as parthenogenetic forms or, rarely, by producing the sexual forms, so that the elm generations are not essential now to the apple generations.

There are other aphides, such as the Spruce-Larch species (*Chermes abietis-laricis*), in which somewhat similar phenomena are observed. This species produces itself parthenogenetically on the spruce and leaves the spruce for the larch to complete its life-cycle and produce the sexual forms, which return to the spruce. Here again the larch is not essential to the continuation of the species which can short-circuit

on the spruce, producing other parthenogenetic generations.

Now in these cases the question arises: Is this the last stage in the reduction of polyphagy to monophagy or is it a distinct phenomenon? It certainly may be argued that the former is the correct explanation, but the point to notice is, that the host upon which the sexual generations are produced is the principal host—in these two cases the elm and the larch, while the apple and the spruce are secondary. If we believe that these species of aphids are on the point of becoming monophagic, we may regard the rare occurrence of the sexual generations on the apple as a remnant of what was once the regular happening and the absence of the occurrence of sexual generations on the spruce as indicating that the spruce-larch species is nearer to monophagy than the woolly aphid. But here in both cases we have an indication of physiological species within the species.

The short circuit, aided by complete parthenogenesis on both the apple and the spruce, is making the apple race and the spruce race independent of the elm race and the larch race, so that in time both these races may become separate true species. It may well be therefore that in many cases monophagy is not so much the result of a species becoming more restricted in the variety of its diet, as of physiological races arising on the different food plants and breaking up what was originally one polyphagic species into several monophagic ones.

So far, therefore, we have seen that the dependence

of insects upon plants for food may indirectly have given rise to new species. But plants may provide food for insects without suffering thereby, and in such cases we find that the plants expect something in return. The production of seeds on a plant necessitates the transference of pollen grains containing the male element from the stamens of a flower to the ovary containing the female element. The ovary usually bears a structure, the stigma, which is sticky, so that the pollen grains readily adhere to it and the grains then grow out a tube which, carrying within it the male element, passes down to the ovary and unites with the ovule.

In the more primitive flowers the wind distributes the pollen, and since the chances of the pollen grains reaching the stamens are very small, the wind-pollinated flowers produce very large quantities of pollen. At the right season of the year the clouds of yellow pollen can be seen being blown from the pine-trees on a sunny day in the British Islands. But early in the history of flower production insects seem to have become useful, and plants began to specialise in two directions to utilise these visitors, for which they began to provide nectar in special glands within the flower and extra pollen as food. In some cases the flowers became massed together so that the inflorescence became conspicuous, although the individual flowers remained small, and this line of evolution was economical in that the mass of flowers formed the attraction and the insect, having arrived, pollinated many flowers within a small area. The elder, hemlock, and daisy are three examples of different groups of plants in which

this massing of flowers has taken place. It has frequently led to a modification of the individual flowers, such that those in the centre of the mass are of different form from those outside: as, for instance, in the daisy, where the central flowers are regular tubes, while the outermost or ray-florets bear the large expansion to the outer side which makes these flowers irregular in form. However it may have been brought about, there is no doubt that the massing of the flowers was an advantage to the plant in connection with insect visits and that the form of the flowers was changed as the result of this massing. In other cases each flower became specialised, so as to ensure that the visiting insect gathered some of the pollen, or, on arrival, deposited pollen gathered elsewhere.

It might be asked, if the flower has both male and female organs, why does it not develop some device of self-pollination, so as to save all this trouble in connection with cross-pollination? The explanation is that there seems to be a law of Nature which holds for most animals and plants that in-breeding is bad for the species and, just as the plants adopt various devices to avoid it, so human beings draw up tables of consanguinity and forbid a man to marry his grandmother. Some plants produce the sexes in different flowers and even on different plants, while most plants ripen one sex before the other, so that, for instance, the stigma is not ready to receive pollen until the stamens of the particular flower have shed what they have produced.

But some flowers might be described as cautious.

The violet, for instance, produces two kinds of flowers : one of which gives nectar and is scented and attractive to insects, while the other never opens, has no nectar nor scent, and sets its seeds without outside assistance. The narcissus and crocus have their stamens so placed that they cover the stigma, and if, as may well happen in the cold weather when these flowers open, no insects arrive, the flower is self-fertile. Various other flowers have moving stamens or stigmas, which change their position as the flower matures, so that the stigmas come into contact with the last ripening stamens and get pollinated in case no insect has brought pollen from elsewhere—e.g., the Lesser Spearweed (*Ranunculus flammula*), *Geranium pyrenaicum*, *Malva rotundifolia*, and others.

But the flowers which have gone in whole-heartedly for insect-pollination have lost this caution and have sacrificed everything to attracting certain types of insect, providing landing stages for them in the form of a large lip, lines of colour so arranged that they are supposed to point to the nectaries, and so show the insect where to find them—hence they have been misnamed “honey-guides”—and elaborate devices by means of which the insect, in seeking the nectar, gets brushed with the pollen from the stamens and rubs itself over the sticky stigma.

If one thinks out this last statement it will appear to be absurd. If the insect gets pollen upon it at the same time as it rubs the stigma, either the pollen gets upon the insect at some part where the stigma does not touch it or self-pollination is indicated. But the flower

overcomes these difficulties usually by ripening the stamens first, so that when the insect becomes dusted with pollen the stigma is not ready to receive it. The flowers have developed various remarkable mechanical contrivances to escape self-fertilisation and to secure cross-fertilisation. Space will not permit us to enter into details, but the reader who is interested may refer to Hermann Muller's (16) excellent book on the subject, or to the small volume by Sir John Lubbock (15) on *British Flowers and Insects*.

The specialisation of flowers in relation to insects has gone so far that many are dependent upon special insects for their pollination, and, without the insects, the plants can produce no seed. The Yucca plant, for instance, is entirely dependent upon moths of the genus *Pronuba*. The flower is not fitted for self-pollination, and, just as the flower has become dependent upon the moth, the latter has become dependent upon the flower. She lays an egg in the stigma of the flower and as the caterpillar has to feed upon the contents of the developing fruit-pod it is essential that the pod should develop. To ensure this the moth visits the stamens and deliberately collects a mass of pollen, which she then carefully applies to the stigma.

The fig-trees produce a most peculiar inflorescence. The green fig, if cut in two, will reveal a cavity which communicates with the exterior by means of a small pore at the apex of the fig. Examination will reveal the fact that the walls of the cavity are lined with numerous minute flowers, the succulent fruit being the swollen end of the flower-stalk, just as the pulp

of the apple is the swollen stalk which has bulged up all round the ovary. These fig inflorescences are the haunt of large numbers of minute wasps (*Blastophaga*), the females of which lay their eggs in certain flowers, and, by walking over the others, transfer the pollen from stamens to stigmas. Without these insects the wild figs cannot produce seeds, and without the figs the insects cannot reproduce. The Monkshood (*Aconitum*) is dependent for its pollination upon the humble bee, and a map of the distribution of plant and insect shows that the range of the aconitum is within that of the bee. When red clover seed was first sent to New Zealand a magnificent crop resulted with abundance of flowers but, to the surprise of everyone, no seed was set. This was due to the fact that humble bees did not occur there, and they had to be introduced from this country.

From what has been said it is quite clear that plants provide nectar and pollen in return for the work done by insects in setting their seed; but there are other plants which provide food and shelter for ants, apparently in return for the protection against other ants and grazing animals provided by these pugnacious little insects. The Cecropia or Trumpet-tree of South America, which grows to about 20 feet in height, has the internodes of the stem hollow, which is not a very remarkable thing, but the nodes provide only a thin layer of tissue between these internodes. The leaves mostly grow at the top, and just above the base of each leaf-stalk there is a slight depression in the stem where the wall is very thin

and soft. The internodes are usually occupied by hosts of a small ant. The queen ant first makes her way into the tree when it is young, perhaps 6 feet high, by biting her way through the weak spot in the wall of the internode. She then settles down in the excellent chamber provided for her and the door through which she has entered rapidly grows tissue and becomes closed. She rears her first batch of less than a dozen workers in the cavity, and, when they become adult, they once more open the door to the exterior. Now the tree not only provides this excellent accommodation, which the ants extend by biting through the thin nodal partitions, but on the hairy base of the petiole of each leaf there develop numbers of small yellow bodies which, so far as is known, are of no use whatever to the tree. These are the food upon which the ants live, and they gather them and store them in the nest in the stem. It appears, then, that the *Cecropia* provides both food and lodging for this particular ant, which is very pugnacious, and, if the tree is in any way disturbed, hordes of individuals swarm out and are ready to attack an intruder. Many trees in South America suffer from the ravages of the "leaf-cutter" or "parasol" ant, which removes the leaves to underground nests, where they are used as soil for the growth of fungi. The *Cecropia* is apparently immune from these attacks, so it is perhaps justifiable to assume that this immunity is due to the presence of the little Azteca ants.

In the same way an *Acacia* in Nicaragua was discovered by Belt (2) to provide homes for ants in large

thorns at the base of the leaves, and also scattered nectaries, producing sweet sap, and small food bodies at the apices of the leaflets, and he suggested that these ants kept the tree clear of the leaf-cutters, and also prevented animals from grazing upon the leaves. And just as plants have become adapted to insects, so the latter have become adapted to plants, the form of mouth-parts being suited to the form of the flowers frequented. Those insects which sip their nectar at the open flowers have short and broad paint-brush-like mouth-parts, while those which visit the long tubular flowers have one or more of the mouth-parts lengthened out so that the nectaries may be reached. Pollen eaters have hairy mouth-parts suitable for sweeping up the pollen grains, and those insects, such as the bees, which gather and store up pollen, have elaborate fur coats in which the pollen grains become caught, and, in addition, some of the higher bees have pollen baskets and special brushes upon the hind legs.

And now to return to the subject of plants as the food of insects. When speaking of parasites in the last chapter, we saw that the ideal parasite did not commit suicide by wiping out its host, and, in the same way, there is a balance between plant-eating insects and the vegetation, so that the former do not become so numerous as to destroy their food materials. We saw, however, that some parasites were apparently destroying their hosts—*e.g.*, the cuckoo-bees—and in the same way there are some plant-killing insects.

The Cochineal insect, mentioned in the first chapter, was introduced into India from Rio de Janeiro in 1795 with a view to starting the dye industry in that country, but either the wrong strain of bug was introduced or, under the different climatic conditions, it was useless commercially. However, it became wild and fed upon the prickly pear (*Opuntia monacantha*), and in twenty years it had practically cleared Southern India of this troublesome weed. In 1913 this Indian Cochineal was introduced into South Africa for the express purpose of destroying this same *Opuntia*, apparently with satisfactory results. The small Lantana Fly (*Agromyza lantanae*) lays its eggs in the immature berries of the lantana, which is its chief food plant. The maggot feeds upon and destroys the seed. Wherever the lantana has reached a country with a suitable climate it has spread very rapidly over waste ground, and is apt to spread where it is not wanted. In Hawaii and certain other places this fly has been exceedingly useful in destroying the weed. It will be noticed that, in the case of the Cochineal insect, it was after introduction to a new country that it became a plant destroyer, and, in the same way, the lantana plant is a native of South America, and the successful experiments in its control by the fly have been in Hawaii, Fiji, and Australia.

An experiment is now in progress in New Zealand, where the bramble is a very free-growing weed. Dr. Tillyard (19) has been introducing numerous bramble-eating insects with a view to destroying the plant. This is a very risky experiment because, under

changed climatic conditions, these bramble-eaters may well turn their attention to some other kind of food, but the principle is justified on what has already been said.

It has already been mentioned that the protoplasm and sap of the plant are the main food of vegetarian insects, and therefore, with a view to preventing insects destroying our food plants, researches have been made upon the sap with a view, amongst other things, to discovering the qualities which attract insects.

The quality of the sap varies from time to time in the individual plant, and observations have shown that where, for instance, Cacao or Citrus are protected from wind or by shade trees, sucking insects, such as Scale, Aphis, or Thrips, are less troublesome than when the plants are exposed to wind and sun. In other words, loss of water, through transpiration of the plant, which increases the osmotic pressure of the sap, favours the insect. Therefore irrigation of cotton has been suggested as a means of reducing the attacks of the cotton thrips in the Sudan. Chemical examination of the sap shows that the quantity of sugars varies, and experiment has also shown that increase in the quantity of reducing sugars is associated with increased damage by insects. In the normal process the sugars in the plant are replaced by organic acids, and increase in organic acids increases the resistance of the plant to insect attacks.

Experiments have therefore been made with a view to controlling the nature of the sap so as to make the plant resistant to insect attack, and the simplest type

of such experiment is treating the ground with some chemical manure. It has been shown in the case of sugar-cane, cotton, and various other crops, that the nature of the soil affects the resistance of the plants to insect attack, and, speaking broadly, we can say that this is largely due to the fact that each type of plant requires certain soil conditions in order that it may attain its maximum vigour and that other conditions affect its health and make it less resistant. Sugar-cane in Trinidad has suffered for many years from the attacks of a small bug, the sugar-cane Frog-hopper (*Tomaspis saccharina*), and in 1914 an entomologist was sent out to investigate the problem. He showed that wherever cane was grown in badly drained soil or under conditions which reduced its vigour the froghopper did the greatest damage (21). More recently it has been found that the acidity of the soil is an important factor, and that on the limestone areas and on limed soil froghopper does much less damage. This may be explained on the ground that the lime affords the ideal conditions for the vigour of the plant or, possibly, and perhaps more probably, the lime acts directly by neutralising the acidity.

In India, the tea-plant is, in many places, seriously damaged by a small bug known as the "Tea Mosquito" (*Helopeltis*), which appears in vast numbers and sucks the sap so that the plants wilt and the leaf is useless. Andrews, the entomologist to the Indian Tea Association, having tried all the usual methods of control of the pest itself, decided to start at the other end and to attempt to make the plant immune

from attack. By careful examination of the soils and the chemical composition of the leaf of the tea-plant he came to the conclusion that, if it were possible to increase the proportion of potash in the plant, the sap would be less attractive to the bug. At first he tried injecting fluids into the plant, a method which had been tried with indifferent success on trees by many experimenters. At this time Dr. Gough, of the Egyptian Entomological Service, made a suggestion which led Andrews to experiment with the roots. He unearthed a small bunch of roots and placed these in a solution of a soluble potash salt. This salt was readily taken up by the roots into the plant, and in about three weeks the plants so treated, which had been badly attacked by the pest, had taken on a new lease of life and were producing fresh leaves undamaged by the *Helopeltis*. It was noticed that the bugs attempted to suck the sap, but that they seemed unwilling to continue, and that the punctures made by the mouth-parts healed up without apparently in any way damaging the leaf (1).

Here then is a new principle of insect control—making the plant immune from attack—and this method has a great future before it. Here again we see that the individual who is going to undertake the control of insect pests has another large field of knowledge to explore. He must have a good grounding in botany, especially in the physiology of plants, and in the relation of the plant to the soil, in order that he may, like a great general, be prepared at all points to meet the attack of the enemy.

CHAPTER V

THE GEOGRAPHICAL DISTRIBUTION OF
INSECTS

WE do not seem to have any good words in the English language for distinguishing between the actual process of dispersal of animals and plants and the result of this process which can be mapped out for each species. I should have liked to head this chapter with the title "Insect Dispersal and Distribution," but, according to the dictionary, it would have been mere redundancy, equivalent to the "erred and strayed" in the Prayer Book.

We may take it that every organism requires a certain amount of space for itself, and that, obeying the law to reproduce its kind, each individual is having to struggle for the requisite space with other individuals, so that there arises the necessity for dispersal. And this necessity for space is backed by the necessity for food, so that we may describe as normal dispersal a spreading-out of a species owing to the necessity for food and space.

And the amount of space required by an individual seems to be unduly large in many cases. For instance, there is a minute water-beetle (*Bidessus minutissimus*), which occurs in certain southern and western districts of Britain and in south-western Europe. Its length is only about 1·5 mm. (about 3/10ths of an inch). I have, on several occasions, kept specimens alive in tumblers

of water, but in every case where more than one specimen has been placed in a tumbler there have been deaths within a short time, and, within a few months, either all have died or only one has survived. But I have kept single specimens alive for three years at a time. We may take it, therefore, that the tendency to crowding due to reproduction—crowding being a very different thing for different species, and perhaps for one species under different conditions—leads to normal dispersal in all directions, so far as this is not prevented by natural barriers such as oceans, climatic conditions, types of country such as mountain ranges, etc., types of vegetation such as forest, etc., each different species being limited by different barriers according to its natural habits. But undue crowding has strange results. Everyone has heard of plagues of locusts, and these are swarms of individuals all migrating together. Egg-masses are buried in the ground by the ovipositing females, and great numbers of individuals lay their eggs within a limited area. The young "hoppers" hatch out and, for the first few days, content themselves with feeding upon the vegetation where they emerge. But as the food-supply becomes exhausted, the migratory instinct suddenly arises and the whole swarm moves off, hopping sedately and feeding and growing, and, when the adult winged stage is reached, continuing the migration by flight. It is now known that there are two phases in the life-history of the locust; one migratory and the other non-migratory and the two are sometimes so different in appearance that they have been described as different

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species. In the case of one species, and it is probably true of others, it has been shown that either phase can be induced, crowding producing the migratory form and plenty of room producing the non-migratory (14).

At odd times, swarms of dragon-flies occur in various parts of the world, and there is a widespread belief that droughts and dragon-fly swarms are in some way associated. The gradual reduction of the water in a pond, owing to want of rain, necessitates the crowding of the inhabitants, and this would probably enable the dragon-fly nymphs to capture food more easily than under normal conditions. This might cause individuals, otherwise not destined to emerge as winged individuals until the following year, to shorten their life-cycle so that two batches would appear together in one season. The food-supply of the adults, which consists of winged insects, would thus run short, and this might lead to migration.

There appear from time to time in the newspapers reports of caterpillars stopping trains, and perhaps some people picture mountains of them through which the locomotive cannot push its way. As a fact, though the numbers are very great, it is the greasy fat of the squashed individuals which makes the rails slippery, and the train is held up because the engine wheels cannot get a grip; but the origin of these swarms of "army-worm," as they are called, is interesting. Examination of a swarm shows that it consists of about 95 per cent. of one species, and that the other 5 per cent. are made up of perhaps nine or ten other species and the explanation seems to be that,

owing to some upset in the balance of Nature, large numbers of the mother moths of the dominant species have survived to lay eggs or large numbers of the caterpillars have escaped parasitisation. Owing to the excessive numbers of caterpillars, the food-supply is quickly exhausted, so that not only the caterpillars of the pest species are affected, but all other caterpillars which normally feed upon the same plants. Starvation causes them all to migrate together as one swarm. It may be that many other migrations of insects are caused by starvation. Each year various species of butterflies reach these islands from long distances. The Painted Lady (*Vanessa cardui*) arrives in May or June from North Africa, and Skertchly has recorded the fact that near Sowakin, in Nubia, in March, 1869, he observed the pupæ of this species so numerous that almost every blade of grass seemed to bear one (18 and 22). And this suggests that in this case also starvation may be the cause, or one of the causes, of the migration. These butterflies, after arriving here, lay their eggs upon thistles, and a fresh generation of adults hatches out about August. But the species never survives the winter here, so that we are each year dependent for this, and a number of other insects, upon the arrival of individuals from some other country. ●

In the cases cited the migration apparently leads to nothing, no obvious extension of range of the species being attained, and yet such migrations may well be successful from time to time when a species reaches some area which is suitable as to climate and other

conditions, so that it can hold its own in the struggle for existence with the native species. The examples given also show that the insect may make its migration either in the young or in the adult condition, or in both. And normal dispersal also may take place before the insect has attained maturity. Gnats and Mosquitoes lay their free floating eggs, the former in small batches or "rafts," the latter singly, and, although many species lay in stagnant water, others do not and such eggs may from time to time be carried far from where they were laid. Their larvæ may be carried by floods, and the adults are known to make migrations between breeding and feeding areas (17).

In certain bugs—e.g., *Diplonychus* and *Belostoma*—the eggs are attached to the upper wings of the male, so that dispersal of these insects commences at once if the male wanders from the mating centre. Some insects disperse in the nymphal or larval condition. For instance, as already mentioned, in the case of some parasites, the young larva has to find its way to its food-supply. The Melœ, one of the so-called "oil-beetles," deposits her small yellow eggs to the number of about ten thousand in three or four batches in holes which she digs in the surface of the ground. In a few weeks the young larvæ hatch out and, after a short interval, they become very active, climbing up the vegetation and getting into the flowers. Here they await the arrival of flying insects and they immediately attach themselves to hairy ones. Their future depends upon their getting upon certain bees and, unless they succeed in this, they perish, and it is

because the chances of success are so poor that the mother beetle lays so many eggs. It is true, in most cases, that large numbers of eggs or offspring indicate a precarious existence before maturity is reached. Thus, the Melöid beetles are dispersed in their first larval stage, being carried to the nests of bees where they ultimately devour the bee's larvæ and the honey paste stored up for it.

The caterpillars of certain moths, for instance the Gipsy Moth, already mentioned, during the first week or two of their lives are the main means of dispersal of the species. The moths are rather heavy and do not fly far. The mother moth lays her batches of eggs low down on the trunk of the tree, covering them with yellow hairs shed from the apex of her body. The caterpillars, when they hatch, possess a number of very long hairs, many of which bulge out into an air-filled vescicle. These little creatures climb to the tops of the trees and allow themselves to be wafted away by the breeze, and experiments, made by setting up wire-netting screens painted with bird-lime or other sticky material, show that these larvæ are often carried great distances from their hatching place. Many insects disperse normally in the adult condition: for instance, fleas, whose life-history has already been referred to (p. 39), attach themselves to their hosts when they attain the adult condition and are carried about by them, dropping off wherever they may be when the time comes for oviposition.

These methods of dispersal so far described are all more or less deliberate, but accidental dispersal plays

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an important part in carrying insects across barriers which otherwise might for ever restrict their range. For instance, winds, especially whirlwinds and hurricanes, and floods may transport insects very considerable distances, especially considering that many of them are very tenacious of life. In mid-Atlantic, on a journey to South America some years ago, various odd insects arrived on the ship from time to time, probably having been caught up by a sudden wind and carried upwards and out to sea. On a recent visit to the West Indies, when between four and five hundred miles out of Avonmouth, numbers of small pyralid moths appeared resting upon the calm surface of the sea and rising up on the approach of the ship. Some of these flew in at portholes, so that I was able to capture them and have them identified. The species* has a world-wide distribution, but it can scarcely be suggested that the numerous individuals had been trying to create a record of crossing the Atlantic. It seems more probable that they were caught up by the wind and carried out to sea. Many insects can safely cross the sea under the bark or in the wood of trees which have been torn from their hold by floods and carried down rivers, as experiment has shown that many withstand complete submergence for long periods, so that such voyagers have an excellent chance of reaching new territory. Man is perpetually transporting insects from place to place. Ships have carried cockroaches, flies, and other insects from one country to another, and market produce has been proved many times to be the source of supply of insect pests.

* *Neomachilis* ...

The Americans indignantly repudiate having sent the Mediterranean Flour Moth (*Ephestia kühniella*) to Europe, but if they did, as seems probable, Europe has supplied them with more pests than it has received from them. The Brown Tail Moth (*Nygmia phæorhæa*) was introduced into the United States about 1890, probably in nursery stock from France, and has been exceedingly troublesome as a pest of fruit-trees. The Colorado beetle (*Leptinotarsa decem-lineata*) has several times reached Europe from the States, and the list of accidentally introduced pests for every country is very extensive.

In order to stop this introduction of pests, each country has now developed a system of inspection of imports, and requires either certificates from reliable authorities that the materials have been disinfected and are pest-free, or more usually that disinfection, usually by fumigation, should take place before the goods are removed from quarantine. Each country has an insect black list, but in this country we have a comparatively small one, because, fortunately, our climate is unsuitable for most of the serious pests: but in warmer countries, such as the United States, the Inspectors of the Department of Entomology are perpetually on the watch to keep out the few remaining first-class pests which have not yet reached them. But the laws with regard to importation of goods liable to bring insect pests into a country are all based upon knowledge of the habits of the insects as acquired by a very careful study of them, and in connection with this importation of pests there is still

very important work to be done. It is easy to fumigate cotton seed, grain, and various other seeds, but many imported foodstuffs cannot be so treated.

At the present time the Entomological Department of the Imperial College of Science in London, under the ægis of the Empire Marketing Board and the Forest Products Board, is carrying out experiments in connection with stored products and timber with a view to reducing the immense losses caused by insects, and for this work men thoroughly versed in the structure and habits of insects are essential.

In conjunction with this work it is important that research should be carried on in the colonies with a view to reducing and eliminating the infection of such goods before they are shipped. The colonies themselves have long realised the value of trained entomologists in controlling the pests of the various crops, and time has shown that the training of these men must be broadly based so that they may be able to work, as Andrews did, not only by destroying the insect pest, but by making the plant immune from attack.

Consequently, whereas not so long ago it was difficult to find posts for enthusiastic entomologists, now it has become difficult to find men for the posts. The present economic entomologists are the pioneers in a work which is going to attract much more attention than it has done hitherto. We have reduced the dangers of malaria, which not so long ago was responsible for half the deaths in the world every year, by controlling the mosquito, and we shall

ultimately overcome the insect menace to our food-supplies and our commerce which, without the aid of the entomologist, would most certainly overwhelm us.

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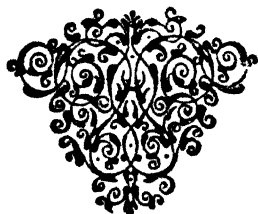
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INSECTS & INDUSTRY

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PREFACE

THIS little book has been prepared for the publishers at the suggestion of Professor Balfour-Browne. Though the subject is treated as a separate volume, it may well be read as a supplement to his *Insects* (No. 45 of this Library), and, it is hoped, will serve to interest readers in a branch of applied biology, which, as the years pass and industry advances, more and more nearly affects their own affairs and well-being.

INSECTS AND INDUSTRY

CHAPTER I

INTRODUCTORY

THE study of the relationship of insects to industry, including agriculture, the oldest of all industries, forms that branch of biological science which is termed economic entomology. Its aims and objects are primarily to assess the nature and cause of the losses inflicted on industry by the activities of insects, to ascertain how far these losses can be prevented or avoided, and to devise practical measures of remedy and prevention.

Economic or industrial entomology requires for its successful practice not merely a knowledge of insects or a knowledge of industry, but a knowledge of the relationship of these to one another, and it calls for ability and skill not necessarily possessed by the academic entomologist. It is a branch of what Francis Bacon called "history mechanical," a branch of "such natural philosophy as shall not vanish in the fume of subtile, sublime, or delectable speculation, but such as shall be operative to the endowment and benefit of man's life."* Its methods are precisely those of his "history mechanical," not only "to minister and suggest many ingenious practices in all trades," but "further to give a more true and real illumination concerning causes and axioms than is hitherto attained."

* *The Advancement of Learning*, Book II.

We have quoted Bacon because there is in some minds a tendency to regard the application of a science to industry as a degradation of that science, and to consider that the methods of applied science are less exact and its standards lower than those prevailing in the academic world. That view of applied science is slowly being dispersed, but it is necessary to remember that it exists because for many years the progress of economic entomology has been retarded by its advocates who were more concerned with "subtile, sublime, and delectable speculation" on their pet theories than they were with the advancement of learning.

Another mistaken conception regarding economic entomology is that it is concerned mainly with the destruction of insects and, in particular, with the destruction of insects by means of poisonous sprays and gases. While it is true that a knowledge of the preparations and application of insecticides is essential to the economic entomologist, it forms only a part of his equipment, and to consider that economic entomology consists mainly in applying insecticides is just as erroneous as it would be to say that the writing of prescriptions constituted the major part of the practice of medicine. As the medical practitioner is concerned with the diagnosis and prevention of disease, so the economic entomologist is concerned with the assessment of the losses caused by insects, with the origins and causes of those losses, and with the devising of ways and means of preventing them. As the scientific study of economic entomology progresses, the present somewhat indiscriminate use of insecticides will be abandoned, and will be no more representative of applied entomology than the time-honoured bottle of medicine is to-day representative of the methods of preventive medicine.

Paradoxical though it may seem, the destruction or annihilation of insects constitutes only a minor part

of the economic entomologist's work. In fact, one of the essential qualities in the economic entomologist is that he should be able to keep insects alive. Unless he has acquired the knowledge and skill necessary for the rearing of insects, knowledge and skill obtainable only with long practice, and even then more often a gift of nature than an acquired skill, he cannot study his subjects nor can he understand them. Adequately to study the habits and life-history of even a single insect is the work of years, and it can be successfully pursued only after many trials and vexations.

Even for the proper study of the destruction of insects by insecticides it is necessary to rear large numbers of them. In some experiments recently carried out in the Entomology Department of the Imperial College of Science, to study the destruction of insects by freezing, no less than two thousand eggs of a small moth (*Plodia interpunctella*) were used in each experiment, and enormous stocks of insects have to be reared in order to secure adequate supplies for experimental work. One of the major items in the cost of equipping the economic entomologist is that entailed in the erection and equipment of special insect houses or insectaries, in which the conditions of temperature and moisture can be regulated to suit the exact requirements of the insects to be studied. This rearing of insects requires a knowledge of many branches of biology, and the up-to-date economic entomologist frequently includes among his staff scientists other than entomologists, whose duty it is to experiment and advise on such matters as the regulation of temperature and moisture conditions in the rearing of insects, the proper preparation and concentration of poisonous gases used in control work, the chemistry of insecticides and the relationship of plant diseases to insect attacks.

It is in the early stages of his work that the

applied entomologist makes most use of his entomological knowledge; in the later stages he may find himself studying agricultural practice, or forest operations, or methods of storage and marketing, for as soon as he is ready to apply his entomological knowledge to industrial problems he must ascertain at which stage in the industry it can best be applied, having due regard to the convenience of the industry, the costs of application, and the prospect of practical results. He can ascertain these necessary facts only by acquiring a first-hand knowledge of the industry and by securing the confidence and goodwill of the industrialist.

In tackling most insect problems the entomologist's methods are much the same, and follow a fairly well-defined line of work. His first step is to ascertain or determine the identity of the insect or insects responsible for the damage or losses caused. Here he meets sometimes with two difficulties. First, it occasionally happens that the insect is an undescribed one, and unless the entomologist is himself very well acquainted with the group to which it belongs he must submit it to an expert and await his report on it. In this country and throughout the Empire the central institutions for the description and naming of insects are the Natural History Department of the British Museum and the Imperial Bureau of Entomology. These two institutions work in the closest co-operation with one another, and form, so to speak, the foundation of our Imperial economic entomological services. The correct description and naming of our insect pests is the basis of economic entomology, because until these pests can be readily identified, and until they have been given a name which all authorities in all countries will accept and use, they cannot be properly referred to in reports or other publications. Fully and correctly to describe an insect is no easy matter. It requires an extraordinarily wide

knowledge of insects in general, and a detailed and highly specialised knowledge of some particular group. The days when outstanding naturalists like Linnæus could profess familiarity with most of the known insects of a continent are long past, and to-day one of the serious causes of delay in the progress of entomology is the lack of systematic entomologists who can overtake the huge task of describing, naming, and classifying the enormous number of insects which our economic entomologists are submitting to museums and institutions throughout the whole world. Of the importance of this work there is no question. Once an insect is identified, all that is known concerning it can be found in the literature of entomology; until it is identified that literature is as a sealed book concerning it.

The correct identification of an insect and the study of the existing information on it contained in the literature are the first steps towards the understanding of all insect problems. One of the most important advances made in the development of entomology in our Empire was the establishment in 1910 of the Imperial Bureau of Entomology, which, in co-operation with the British Museum, insures the proper identification of our insect pests, and by the publication of the now indispensable *Review of Applied Entomology* enables the economic entomologist, even in the remote outposts of the Empire, to keep abreast with the recent literature of his subject and the new knowledge it has to convey.

The second difficulty encountered by the entomologist facing a new problem is to ascertain precisely which of the many insects he finds associated with the losses he is investigating is the primary and direct cause of trouble. This is by no means so simple as it may appear, and A. S. Packard, one of the first American forest entomologists, has related how, when investigating the dying of the coniferous forests of the

eastern United States, he ascribed the dying of the trees to the work of certain bark-boring beetles which occurred in tens of thousands, and completely overlooked the real and primary cause of the damage—namely, the so-called "spruce bud-worm," a Tortricid moth (*Cacæcia fumiferana*), which by the time he visited the district had left it for fresh woods and pastures new.

Such instances in which the attacks of a primarily injurious insect are followed by an increase of insects of secondary importance are especially frequent in forest entomology, but they may occur in all industrial entomological problems, and must always be expected and studied.

Sometimes it happens that one has to tackle other insects than the primarily injurious one. In Kenya one of the insects most injurious to coffee cultivation is a scale insect, the "Mealy Bug," (*Pseudococcus citri*). This insect can be kept in check by the use of insecticides, and by encouraging certain insects which are predacious and parasitic on it; but even when a plantation has been sprayed and rid of the Mealy Bug, an ant (*Pheidole punctulata*) carries the bug into the plantations again and so reinfests them. This ant obtains a sweet secretion from the Mealy Bug and so tends it and farms it out on the coffee bushes. *Pheidole punctulata* also destroys the predaceous and parasitic enemies of the Mealy Bug, and the problem in Kenya is now just as much how to destroy the ant (*Pheidole punctulata*) as it is how to destroy the Mealy Bug (*Pseudococcus citri*).

In ascertaining the cause of damage to a crop or product, the problem is not always to distinguish as between one insect or another as the real source of trouble. Not infrequently, as in agriculture and forestry, the difficulty is to decide whether the failure or destruction of a crop is really the result of insect attack at all, or whether the original source of trouble

may not arise from unfavourable soil conditions, or from the attacks of some fungus or bacterial disease, or even from both these factors together.

In the larch woods of the South of England one frequently finds dying trees occurring here and there in groups, which, on inspection, are found to harbour the grubs of a long-horned beetle (*Tetropium gabrieli*). Formerly it was thought that this beetle was the cause of the larch dying in many districts. We now know that the beetle is only of secondary importance, and that its presence is almost invariably an indication that the soil conditions are bad, and that in consequence root rot in some form has set in.

Tetropium gabrieli is a favourite food of the woodpeckers and these birds peck and hack at the bark of infested trees to get at the *Tetropium* grubs. In doing this they expose the richer red of the inner bark of the larch, and their work can for this reason be seen from a long way off. To the knowing forester it calls attention to the presence of the *Tetropium* beetle, and frequently enables him to recognise that soil conditions are amiss when otherwise he would quite excusably overlook them for quite a long time. Dense larch woods are not easily traversed or inspected, and the *Tetropium* beetles, by attracting the woodpeckers, which in turn attract the attention of the forester, are actually more beneficial to his interests than they are injurious.

Bearing in mind all these complex relationships of insects to one another, and of insects to plants, and plants and soil conditions to insects, the entomologist ascertains just which insect is the most important in relation to his problem and decides to tackle it. His next step is to study its habits and life-history. It may be that in looking through the literature relating to it he finds that its life-history has been described or partially described or "worked out." If the description is full and detailed and gives the particular

information wanted as a basis for the study of control measures, a new study of the life-history may be unnecessary. Even so, the experienced entomologist invariably checks up or "confirms" the work of his predecessor, at least in so far as it relates to the salient features of the life-history or to points of special importance for his particular problem. His object in doing this is to insure that he may devise the best kind of control measures, and apply them at the time or times when the insect is most vulnerable.

If the published accounts of the life-history are too meagre or too general to form a sound basis for the devising and application of control measures, then the insect must be studied anew. In doing this the entomologist may use previous work as a general guide, although in actual practice it is sometimes wiser and safer to ignore previous work all together.

One of the surprising features of economic entomology is our meagre knowledge of even our most important pests. In this country, for instance, we have no complete account of such common pests of agriculture as the "wireworms," the larvæ or grubs of certain Elaterid beetles, although these insects have been known to generations of farmers and exact a heavy toll of all their crops. The same holds true almost for the majority of our native insect pests, and one of the crying needs of economic entomology in this country is for better, fuller, and more fundamental studies of insect life-histories.

The reasons for the neglect of this biological work are various. In the first place most of our entomological work is done in the universities or in research institutions linked up to the universities, and as the university summer terms end just when insect activity is at its height in this country, the investigator must either relinquish his work or his vacation. Too often, perhaps, the work is relinquished. Again, to study an

insect's life-history properly requires several years' work. Failures in rearing experiments are frequent, and these prolong the time necessary for a complete study, while the young investigator, who is frequently aspiring to some higher degree, is better advised in its interest to undertake some anatomical or morphological research, which he can abandon and resume again at will, independently of the seasons and with fairly certain assurance of "results" in one or two years' time. Entomological literature is strewn with half-finished biological studies, and for one really useful paper on the life-history of some important insect there are usually half a dozen relating to its structure and anatomy. For example, Straus Durckheim's exhaustive monograph on the anatomy of the common cockchafer was published in 1828, but an equally thorough account of its life-history is still to be written.

It is neither desirable nor necessary further to discuss that matter here, but it is important to note that for various reasons the teaching and study of the identification and classification of insects (systematic entomology) and of the habits and life-histories of insects (insect ecology) are neglected in our universities, and that these two branches are the basis of all sound entomological investigation and research.

To those who in their younger days reared silkworms and puss moth caterpillars, the rearing of insects may seem a relatively simple matter requiring no great philosophy and no great technical skill. When, however, insects, some of them often extremely small and delicate, have to be reared in large numbers and studied in all their stages from egg to first stage larva, and so on to the adult insect, the task is by no means easy.

In the first place the insects must be kept from flying or crawling away, and, although confined, must be kept under conditions as nearly resembling those

of their natural habitat as possible. Some insects will not mate in too close confinement, or, if they mate, fail to leave offspring. Then they must be fed, and many insects are extraordinarily particular in their selection of food. If the food is a plant it must be kept fresh or frequently renewed, if it is some substance such as cheese or dried fruit it must not be allowed to grow mouldy nor must it "dry out." Some insects require moist atmospheric conditions, others prefer dry. Many insects bore in bark and wood, and if removed from their burrows for purposes of study cannot be induced to re-enter them. In actual practice the successful rearing of insects and the building up of large stocks of them is one of the strictest tests of the entomologist's ability. Time and again stocks diminish and die off for no apparent reason. Parasitic insects, moulds, and predacious mites invade their breeding quarters. The night watchman or the caretaker turns off the heat from the insectary or incubator where some specially precious batch of caterpillars are being carefully nursed, or, if one is engaged in field work, wireworms or cockchafer grubs destroy a batch of carefully reared food plants or unexpected frosts kill both food plants and insects.

These and many other accidents test the entomologist's philosophy, and meanwhile his client the "practical man" is shouting for results.

When the habits and life-history of the insect have been studied, the entomologist usually "confirms his results"—that is to say, he repeats his work—at the same time correlating the results obtained in the laboratory or insectary with observations made "in the field"—that is, in the insects' various natural habitats. The term "field work" is used for such work, whether it is conducted in a field, a forest, or a factory.

At this stage the entomologist should have acquired the following information :

1. The identity and zoological position of the insect concerned, together with a knowledge of its country of origin, distribution, and economic status.
2. The host plant or food of the insect, its methods of pairing and egg-laying, its normal rate of development and increase, and the appearance and distinguishing characters of all its various stages.
3. Its relation to the crop or product on which it feeds, its natural enemies, and its general reactions to weather conditions and industrial practices—*i.e.*, how it spends the winter, when it appears in spring, and so on.

When all this information has been acquired the entomologist is in a position to consider the ways and means of "controlling" the insect—that is, of reducing or preventing its depredations. The economic entomologist rarely exterminates an insect, such extreme measures being successfully achieved only by collectors of rare butterflies.

The first and most obvious step in this direction is by means of better hygiene. The burning of stubble and weeds on the farm, the pruning of dead wood and cleaning of lichen off the trees in the orchard, the removal or burning of brushwood or "slash" in the forest, the sweeping of the flour mill or the chocolate factory, the "cleaning up" of the timber yard; all these measures mitigate against the breeding of insects, and, if frequently and thoroughly carried out, go a long way towards reducing insect infestation in general. Unfortunately such measures are rarely popular with or satisfying to the entomologist's client. Something more drastic and more spectacular and difficult is wanted. It is, too, quite often necessary, and so we come to the next line of attack, an attempt to mitigate the insect nuisance by some

slight modification of industrial practice. Improved tillage and drainage, richer manuring, the rotation of crops, and the practice of early or of late sowing, are modifications of agricultural practice, which assist in controlling the increase of insect pests or in "dodging" their ravages. In forestry the regular thinning of woods resulting in the early removal of dying and dead trees, the rapid removal and "conversion" of felled timber, and the growing of "mixed" woods (comprising several different species of tree instead of pure woods consisting only of one species) are well recognised methods of insect control, and are at the same time sound "silvicultural practice."

In the timber-yard, proper piling of lumber, seasoning of the timber by means of the steam kiln, and regular overhauling or inspection of stocks are valuable preventive measures against most of the insects which attack timber.

In dealing with insects affecting foodstuffs and other plant and animal products stored at our docks and warehouses, such measures as the regular periodic fumigation of barges and lighters, frequent white-washing or distempering of wharves and stores, improved ventilation, lighting, and heating of such premises, and systematic grading and segregation of produce are within the power of most business firms and are well worth their extra cost. The day is coming when the more enlightened manufacturers, merchants, and brokers will insist on these measures as part of the normal duties of the wharfinger and warehouseman.

Even in the humble sphere of the household cleanliness, good ventilation, and central heating will confer a freedom from insect pests, which is in too many dwellings still unattained. Lice, fleas, cockroaches, bed bugs, and flies owe their unwelcome presence in houses to the lack of cleanliness and lack of attention on the part of the ignorant or indolent householder

to such matters as the airing of clothes and bedding, the scrubbing of sinks and pantries, and the emptying of the dustbin.

If such hygienic measures and improved practice fail to cope with the insect problem, the entomologist has to resort to more strictly technical methods. These are described in later chapters.

CHAPTER II

DAMAGE AND LOSS CAUSED BY INSECTS

WITHIN recent years the part played by insects in reducing the volume or value of our crops and stores has been increasingly impressed on governments and public bodies.

The war impressed upon private soldier and War Office alike the importance of the contemptible louse, which on the Western Front alone was during 1917-18 responsible for more than one-half of the inefficients withdrawn from the front line to the rest camps or bases, and acting as a vector of trench fever and typhus was in great part responsible for the collapse and distress of the Serbian armies. On the other fronts, and particularly in Salonika, the mosquitoes, the carriers of malaria, proved a very grave menace to our troops, and the attitude of the average army medical officer towards insects and entomologists underwent a remarkable change from 1916 onwards.

Medical entomology received greater stimulus and greater encouragement during the latter half of the war than it had ever received, and although some of the lessons taught are here and there forgotten—as is shown by the present neglect of the malaria problem in

certain of our colonies and dependencies—the status and facilities for work of the medical entomologist have enormously improved.

It was not in medical entomology alone, however, that the war stimulated the study of insects. Our food supplies were threatened and, in particular, large stores of grain were so rapidly destroyed by such insects as the grain weevils and flour moths that had the war been much longer prolonged these insects might well have become the deciding factor in our victory or defeat.

The war, with its peculiar economic conditions, may be regarded as an exceptional period when the insect menace became acute, but, as Dr. Howard, the former Director of the U.S. Bureau of Entomology, has pointed out, the insect menace, while acute during the war, is rapidly becoming chronic in times of peace. He has suggested that the next big war for civilisation may yet prove to be the war between man and the insect, and even allowing for Dr. Howard's enthusiasm for economic entomology and for his desire to secure appropriations for his wonderful entomological service from hard-headed senators, one has to admit that the menace of insects to our crops and stores is no mere bogey, but is one of the alarming phenomena of our present-day civilisation and trade. To ignore the beneficial changes brought about by the war in the way of improved means of communication and trading facilities and of higher standards of living is no longer possible; but it is equally important that we should try to realise that if man has gained by these advances so has the insect, and that it is steadily entering into competition with man in the vital struggle for food supplies.

From the days of the Pharaohs and the locust plagues of the Scriptures, man has been aware of the capacity of insects for destruction, but nearly always he has been interested in the spectacular, and only

when the insect menace assumed plague dimensions was it given serious attention. Plagues or mass outbreaks of insects such as locusts still occur, as they did in the time of the Pharaohs, but spectacular and destructive as these plagues are, they are to-day less important than the less spectacular and less known ravages of insects which as yet have never received popular or common names—drab, insignificant-looking insects, some of which are not even well known to, or properly described by, the entomologists themselves.

The locusts, with their spectacular migrations and voracious habits, represent only one aspect of the insect menace. The drab coloured grain and flour moths, the dull parti-coloured fruit moth (*Plodia interpunctella*), the dingy grain and rice weevils, the unattractive caterpillars known as cotton boll-worms and cutworms, and the fruit flies (almost unknown except to students of the Order *Diptera*), represent another and even more serious aspect of it. These insects live in or at the expense of our food and clothing supplies just as much as do the locusts, and the losses they cause are in the aggregate of much greater significance in our modern civilisation.

The damage and losses caused by insects belong to two categories. There is the periodic and spectacular destruction caused by such insects as the locusts, and there is the steady concurrent and insidious destruction caused by such obscure insects as the grain weevils and clothes moths which attack our stores, the codling moth, and the fruit flies which attack our food supplies, the cutworms and wireworms, which annually take heavy toll of our agricultural crops, and the powder post beetles which reduce some of our furniture timbers to mere powder.

In endeavouring to assess the extent and importance of the damage caused by insects it is useful to bear these two categories in mind. The destruction

caused by locusts and by such insects as the leaf-eating beetles and by the migratory caterpillars known as "Army Worms," from their habit of marching abreast as they feed, is readily assessed, and bears a fairly close relation to the amount of food eaten by the insects concerned. The destruction caused by grain weevils, clothes moths, and powder post beetles extends far beyond the amount of food or stores actually consumed by them.

In the first case, the amount of food consumed or destroyed represents approximately the loss caused. In the second case, the loss caused can be assessed only after careful investigation of many factors. The common clothes moths of our cupboards and wardrobes serve to illustrate the complex nature of such an investigation. A tiny hole, the size, say, of a three-penny piece, gnawed in a "length" of "material" by a clothes moth caterpillar while the "material" is still on the cutter's table, may be a mere bagatelle involving only a little extra thought or skill for its elimination from the final garment, but a similar small hole gnawed in the exclusive model gowns designed, cut, and finished for the Ascot races is a really serious matter. It means not only the rejection of the garment and the loss of the time and labour expended on it, but if the garment has been "delivered" to some fastidious customer it may result in serious loss of prestige for the firm which supplied it. In such a case the loss involved far exceeds the small amount of material actually consumed by the insect, and the consumption of six-pence worth of cloth may mean the loss of hundreds of pounds.

Because of this question of prestige or reputation the losses caused by insects in the manufacturing industries often attain almost incredible dimensions. It is true that the losses are in a sense artificial, but they have nevertheless to be borne, and are some-

times the only means of making the manufacturer realise his responsibility towards economic entomology. In one important industry in this country the occurrence of many kinds of insects in a staple article of food was wholly ignored until recently by every branch of the industry dealing with the raw product. It was only when the stray and chance occurrence of one of these insects in the finished product offended the taste and appetite of a customer and so brought the prestige of the trade in question that the prevalence and occurrence of the insects in the raw material received serious attention.

In the United States of America, partly as a result of the pure food campaigns, partly because of their tariff regulations, and partly because of their fear of introducing noxious insects into the country, the Federal and State governments insist on rejecting insect infested foodstuffs, but in Britain we are still ignorant that the raw materials of many foodstuffs are infested by insects, and so long as these insects do not appear in the finished product we are happy to remain ignorant.

How long we shall be allowed to continue to ignore the depredations of insects in our foodstuffs and raw materials of industry is uncertain, but the day cannot be long distant when the public at large will be aroused to the extent of the insect menace. In the United States various authorities have published from time to time estimates of the loss caused by insects. In Britain, while occasional attempts have been made to estimate the losses caused by such insects as the blow-fly or sheep maggot and the ox-warble fly, no general estimate of the damage caused by insects to agriculture or forestry or to the manufacturing industries and commerce can readily be made. In America, where vast acreages are devoted to one kind of crop—such as cotton or fruit—and where the timber industry is well organised, it is

more easy to assess losses and collect information than it is in this country. Again in the United States, because of the introduction of such insects as the Gipsy moth, the Cottony Cushion Scale, and the European Cornborer, insects not native to America and which in their new environment increased prodigiously, threatening important industries, popular interest in insects is easily aroused, and politicians seeking excuse for the imposition of high tariffs or even prohibition of imports have not hesitated to use the introduced insect pest as a means of overcoming opposition to, or of arousing enthusiasm for, their schemes.

In Britain, we, too, have suffered from the introduction of injurious insects, notably from North America, but as these introductions have seriously affected only our forest and timber industries, neither of which looms large in the public eye, they have passed unnoticed. The result is that at present the public and the politician pay little attention to insects. The farmer who annually suffers loss from wireworm in his grass-land accepts the position. The timber importer who inadvertently buys a consignment of wormy timber passes it on if he can, and the loss becomes distributed over the whole industry, and so distributed is less severely felt than it would be if it fell all on one branch of the industry.

Times are changing, however, and the recent history of the relationship of insects to certain branches of the timber industry illustrates a development which is slowly taking place in many industries. In that section of the timber industry which is concerned with the making of furniture, two valuable timbers are ash and oak. Our own supplies of these timbers form only a very small proportion of the total needed by the industry, and the chief source of the major part of the supply is the United States. During the war this source was temporarily closed for lack of

shipping transport. All our ships trading with America were needed to bring us food, and meanwhile the stocks of oak and ash timber in the United States accumulated. Now in these yards the most serious cause of waste in these timbers are certain small beetles of the genus *Lyctus*, known in the American trade as "Powder Post Beetles." These beetles breed in partly seasoned ash and oak, and when, by the accumulation of stocks of the timbers resulting from lack of shipping, their breeding ground was enormously increased, they too increased in numbers. When trade with this country was resumed after the war large supplies of *Lyctus* infested timber were shipped to this country and were distributed throughout our importing yards and furniture factories. Because in the early stages of attack and because during the cold winter months the presence of the *Lyctus* beetle is not easily detected, the full effects of this widespread dispersal of the beetles or their grubs was not realised at first. The importer passed the damaged goods to the merchant, who passed them on to the manufacturer. He in turn passed them on to the furniture retailer, who passed them on to his customers.

In time each stage of the industry began to realise the evil that had befallen it, but the importers, merchants, and manufacturers hoped for the best and although now and then they protested or refused to accept infested timber, the American interests declared that they had no responsibility in the matter. In time, however, the customer rebelled, and his protests, because they affected the prestige of the retailers, gradually became effective and to-day the whole industry is engaged in an effort to eliminate the *Lyctus* beetles as a source of loss and is attaining considerable success.

A similar sequence of events is occurring in other industries, but so long as losses or damage can be

passed by one branch of industry to the next, none of the participants will consider it necessary to take action. So long as the consumer, who is the general public, is ignorant of the state of affairs, insect infestation of our foodstuffs and raw materials will continue unchecked. The losses are borne by the consumer, who pays a slightly larger price for the finished commodity in order that the various branches of industry may recoup themselves for any loss or trouble accruing from the infestation of their raw materials. In one important food industry, one section of it alone—dealing with the produce of only one part of our Empire—spends £20,000 annually in eliminating or reducing insect infestation, and that sum is of course ultimately paid by the consumer in the form of higher prices. Apart from the still higher price paid for insect infested products, the consumer further loses in that very few food products can undergo treatment for the elimination of insects without suffering at least slight deterioration, and the result of insect attacks on our foodstuffs is both to increase their price and lower their quality.

Apart from being sources of loss because of the food or material they consume, or the injury to business prestige they cause, insects may be a source of other forms of loss. Not infrequently the infestation by insects of some imported commodity results in serious delay in marketing, and goods specially despatched from overseas to reach our ports at "the top of the market" may, because of the delay involved in cleaning or sterilising them, "lose the market" and fetch much lower prices than they should have done. If possible this form of loss is also passed on to the consumer in the form of generally higher prices demanded for subsequent consignments or for consignments of lower quality. Not that the consumer is always the defenceless victim of the merchants or that he is deliberately victimised,

but that in all business transactions allowances have to be made for risk of loss, and almost the only means the seller has of making them is to readjust his prices. Not infrequently the overseas producer suffers, and we are only now, and mainly because of the publicity work of the Empire Marketing Board, beginning to realise how big a part insects play, not only in the production of the raw materials of our industries, but also in the marketing of them. In one important branch of Empire trade in which our chief competitors are the Greeks and the Americans, not only are we handicapped by long distance of transport, but that very long distance transport so favours the attacks of insects that if it were not for the subsidy of the industry by Government, the attacks of the insect (the moth *Plodia interpunctella*) would render competitive marketing impossible. In the building up of that young and growing industry the chief difficulty to be overcome is not the climate or cultivation or labour, but a feeble insect.

Insects may not only cause delay or difficulty in marketing, but they may even govern the market itself. In Central Europe, when periodic massed outbreaks of the Nun moth occur in the spruce and pine forests, so much timber is "killed" that it gluts the market and prices fall with a rush.

One of the most interesting aspects of the damage or loss to man and his property by insects is that relatively few of the many thousands of kinds of insects which are known to science are injurious. Of the twenty-three Orders or major groups of insects now recognised by entomologists only seven or eight of them include insects which are injurious and even in these Orders the noxious insects are comprised only in a few families. The zoological or systematic position of an insect offers no indication as to its potentialities as a pest. Such characters as

size, form, and colour bear no relation to the capacity of an insect to inflict injury or cause damage. Most of the really injurious insects are small and inconspicuous, and neither their general nor their detailed or minute structure afford a clue as to their economic importance. The notorious cotton Boll Weevil (*Anthonomus grandis*), which has at times been responsible for the destruction of half the American cotton crop, differs only in minor and structurally unimportant characters from other members of the genus *Anthonomus*, some of which are of no economic importance whatever.

The truth is, of course, that the terms "injurious insect" and "pest" are purely anthropomorphic terms. So long as the cotton Boll Weevil confined its attention to uncultivated wild plants, such as *Hibiscus*, it had no economic significance. It is only because it found ideal and extensive breeding grounds in man's cotton crops and because of man's methods of cultivating cotton over a vast extent of territory that it acquired and assumed its present position as one of the major insect pests of agriculture. The Colorado Beetle (*Leptinotarsa decemlineata*), an insect whose advent in Europe has on more than one occasion created panic among potato growers, was originally a harmless insect living on wild plants of the Order *Solanaceæ* in the foothills of the Rocky Mountains. It was not until the westward spread of the American settlers and the extended cultivation of the potato had afforded it a vast and extensive breeding ground that it became an object of interest and serious concern to the agriculturist.

The capacity of an insect to become a "pest" is no vice inherent in the insect itself, but is almost wholly dependent on external circumstances created by man's endeavour to control Nature and wrest from her an ever increasing food supply. The really important factor which decides whether an insect has

the potentialities of a pest is its capacity to reproduce and increase rapidly in numbers under the artificial conditions created by man himself. Many of the insect pests of to-day were, not so very long ago, harmless scavengers, or at most humble plant feeders, playing an orderly part in adjusting the balance of nature; breaking down dead plant or animal remains, serving to check the undue increase of plants in the primeval forest, steppe, or tundra, or of some insect or other animal living in these environments, or serving as the food of some predacious insect or other insectivorous animal.

It is useful to remember this origin of our insect pests, and to note that the Colorado Beetle, the insect whose advent and extremely brief stay at Tilbury some years ago gave rise to our Diseases and Insect Pests Acts, was originally a harmless leaf-eating beetle living on the wild relatives of the potato. Some of the most common pests of our stored food supplies, such as the little Silvanid beetle (*Oryzaephilus surinamensis*) were once, and indeed still are in their wild state, bark dwelling insects usefully serving Nature as harmless scavengers.

The reason why such insects have now come to be designated pests is that they found in the artificial conditions created by agriculture and industry opportunities for their unusually rapid reproduction and increase. It is scarcely necessary to remark that one or two insects in a wheat-field or a granary are of no importance but that hundreds or millions of them are, and one of the main duties of the economic entomologist is to study the increase of insects and the various factors both natural and artificial which promote it. We no longer regard outbreaks or plagues of insects as visitations of Providence. We know that insect pests, however noxious, are not isolated entities with an inherent capacity for destruction, but are part and parcel of a biological complex regulated by

many different factors which can be recognised and investigated.

The more important of these factors may now receive consideration.

CHAPTER III

THE ORIGINS AND CAUSES OF INSECT OUTBREAKS

THE investigation of the origins and causes of insect outbreaks is the most important and also the most interesting part of the work of the economic entomologist. It is a part of his work which in the past was sadly neglected, and is even to-day insufficiently appreciated. There are several reasons for the neglect of the study of the causes of insect outbreaks. In the first place their investigation is difficult and time-consuming. Then, faced as he always is with the insistent call for practical control results, the entomologist is tempted to take a short-cut in an endeavour to achieve these, and may consider that he will acquire more credit by relieving a pressing need than by spending time and money in the difficult endeavour to get down to root causes.

The periodic occurrence of insect outbreaks is itself an important cause of the neglect of their proper investigation. Even the most severe insect outbreaks ultimately subside and are forgotten, and it is often extremely difficult for the entomologist to keep up the enthusiasm of his clients or financial supporters in investigating the ecology of an insect whose activities are in abeyance. Frequently some other insect is calling for attention, and it is difficult to disregard it.

Equally important as a reason for the neglect of the fundamental investigation of outbreaks is the general attitude of the farmer, forester, or merchant,

and of the general public. Even to-day their attitude, not much more enlightened, is that of our forefathers, who believed that plagues of insects were visitations of Providence, catastrophies beyond the understanding or control of man. The writer recalls his first meeting with this attitude, and the devastating effect it had on his hopes of obtaining the co-operation of the practical man in an investigation of outbreaks of the oak leaf roller moth (*Tortrix viridana*). During 1920-1924 this pretty moth defoliated the oak woods throughout the whole of the South of England. Its ravages, combined with the attacks of the oak mildew, assumed alarming proportions, and large numbers of valuable oaks were dying in consequence. Practical remedial measures seemed unattainable, and the best way of justifying the writer's position as an official entomologist seemed to be to investigate the progress of the *Tortrix* outbreak, in an endeavour to estimate its possible period of duration and the prospects of its hoped-for early collapse. In the early stages of the work progress was fairly rapid. The habits of the moth were studied, the places where its eggs were laid were discovered to be, not the buds as had been assumed, but the nodes or knots of the young shoots some two or three inches below the terminal buds. The habits of the young caterpillars were watched, and it was ascertained that if they were to survive it was essential on hatching that they should reach the young leaves just as these unfolded from the bud scales. The newly hatched caterpillars could not bore into unopened buds, nor could they successfully attack leaves which had become toughened by a few days' growth or expansion. Parasites of the caterpillars were reared, and the time came when the laboratory had yielded all the results it could, and it became desirable to check these results with events in "the field" or woods. In particular it was thought to be useful to ascertain the variation in intensity of attack which

was observed in different localities. Such information would throw light on some of the causes of this variation, which was thought to be due to the parasitisation of the caterpillars by different kinds of parasitic insects.

Three localities were chosen for this work, and in two of them good progress was made. The foresters were interested in the work and helpful. In the third locality things seemed to hang fire. Consignments of caterpillars required for the study of the intensity of parasitisation failed to arrive, or arrived dead and too shrivelled for study, and finally a diplomatic visit to the locality was made. A long summer day was spent in the stifling leafless woods, and then when the necessary collecting was done the writer sat down with the forester for a tardy meal. The objects of the work were explained, and the difficulty of devising any practical control measures, but this failed to strike any note of understanding or sympathy. Finally the subject was changed, and the suggestion that the broiling dry weather, though unfavourable to tree growth, would be appreciated by visitors to the Ascot races then in progress, immediately brought response from the forester. He explained that there was only one hope of controlling the *Tortrix* plague, and that was to change our hearts and reform our ways. The plague was retribution for our post-war extravagance and levity, such as "bobbed" hair and Sunday motoring. Short skirts had not then "come in," or they, too, would doubtless have accounted for the presence of a few thousand caterpillars! Artificial efforts, said the forester, were bound to be useless and unavailing, and a scientific explanation of the causes of the *Tortrix* plague was evidently to him both wrong and impious.

So extreme a belief in a retributive Providence is not often found nowadays, but, nevertheless, many of the beliefs expressed to-day regarding the causes of

insect outbreaks are only milder forms of it, and, consciously or unconsciously, are derived from it. Sometimes the east wind is held responsible for plagues or blights, as when in late summer swarms of greenfly are observed in our gardens. The greenfly have been there all the time crawling and feeding on our roses and other plants, but, because they remained in compact masses under the leaves or clustered round the stems, were unnoticed. As the summer advanced and the plants become drier and more "woody" nourishment became scarce, a phenomenon hastened by cold, drying winds. These winds, by causing a lowering of temperature, also stimulated the greenfly or aphids to produce winged forms, which then left their impoverished host plants to seek others, and by their apparent sudden appearance gave rise to the belief that an invasion had taken place or that the east winds had produced a blight.

One of the axioms of economic entomology is that, like the poor, injurious insects are always with us, and outbreaks of insects rarely arise by a sudden invasion from some distant quarter, but are the direct result of the steady increase of the ever-present but unobserved few. This may seem improbable to one who is present only when an outbreak is at its height, but the truth of the axiom can readily be demonstrated. It is astonishing how little we observe the numbers of any common insect around us. In a tour of the garden we may with attention observe, say, three or four blue-bottle flies, but if we put down in some spot a piece of raw meat it will soon be covered with these flies in tens and twenties. The short time in which they have assembled shows that they cannot have come from afar, but were present in the immediate vicinity. Examine the piece of meat some hours later, and it will be seething with maggots, which, if undisturbed, will in a few days' time develop into flies, and increase the local popula-

tion a hundredfold. In such a simple experiment we can, by increasing the blue-bottle's food supply or breeding-ground in the form of raw meat, lay the foundation of a blue-bottle outbreak on a small scale. If we continue and extend the experiment we can learn some other important facts concerning insect outbreaks. For the first day or two the blue-bottles will be the only kind of insect on the meat, and they will reproduce and increase in numbers very rapidly. By and by other insects will appear like the big-jawed, black and tawny-grey Cock-tail or Rove Beetle, and the black and orange Burying Beetle. These will eat some of the meat, but they will also attack the Blue-Bottle maggots. Then some tiny, shining, four-winged flies may appear. These are parasites of the Blue-Bottle maggots. Their presence, and that of the Rove and Burying Beetles, slows down the rate of increase of the blue-bottles, partly because there is competition for food between the beetles and the Blue-Bottle maggots, and partly because the beetles and the parasite attack the maggots themselves.

But there are other agencies at work which affect the progress of the developing outbreak we have started.

The Blue-Bottle flies are actively engaged in egg-laying only in warm, sunny weather; cloudy skies and cold winds retard their activities. The rate of growth of their larvæ or maggots is greatest when the temperature is high and slows down in colder weather. Heavy rain disturbs their movements over the meat, and may even drown them. When the Blue-Bottle larvæ are full grown they leave the meat and burrow into the soil, where they pupate enclosed in their skins, which become toughened and barrel-shaped. If the soil under the meat is free and open the burrowing process is easy; if the soil is hard and compact the larvæ may be unable to burrow, and may shelter immediately under the meat or may wander in search

of more open soil. In their wanderings they run the risk of being devoured by predacious beetles or beetle grubs.

If our experiments are delayed until, or prolonged into, late summer a marked slowing down of the development and the rate of increase of all the insects in the community we have established is noticed, until when the frosts become severe activity ceases and all the insects seek winter quarters in the soil or shelter in some protected cranny until spring.

One other point may be noticed in our experiment, namely, that in warm, dry weather, and especially under a hot sun, the meat we supply becomes dried and shrivelled and ceases to attract the Blue-Bottles, and becomes unpalatable to their larvæ, which wander off or succumb to the scorching heat. Incidentally they dislike strong light and are negatively phototropic.

If, now, we review our observations we find that several agencies govern the rate of increase of the Blue-Bottles. The weather or climatic conditions in which temperature, humidity, and light are separable as distinct factors, affect both the insects and their food. The food itself is important. If it is withheld the Blue-Bottles must go elsewhere or starve, and their larvæ, if only partly grown, usually starve, even though some become cannibal, eating their more impoverished or dying associates. The predaceous beetles and parasites also play a decisive part in regulating the Blue-Bottles' numbers, and finally the soil conditions affect the well-being of the Blue-Bottle community by affording a suitable or unsuitable medium in which the maggots may undergo the critical period of their final metamorphosis or pupation.

Now these factors—climate, food supply, natural enemies, such as predators, and parasites, and soil conditions—whose effects we have traced in our experiment, are the chief factors which regulate the increase in numbers of all insects. They act in this

respect both directly and indirectly, and interact among themselves. The climatic conditions act not only directly on the insect itself, but if it be a plant-eating insect they act on it indirectly by regulating the growth of the plant, which is its food supply. The study of this combination and interaction of these primary factors is one of the most fascinating branches of economic entomology. It is now honoured with a name to itself and is described as insect ecology or "autecology." The term ecology is applied when one studies the association of insects in some particular type of environment or "plant association," such as a damp oak wood, or a chalk pasture, and autecology if one studies the plants and animals associated with some particular insect.

If we are to understand the insect pest we must know something of its environment, and to learn something of that it is useful to consider the factors which constitute or produce that environment. They are the same factors which we discovered in our experiments with the Blue-Bottle flies and the meat, which were really a lesson in the autecology of the Blue-Bottle fly (*Calliphora erythrocephala*). If we consider each of these factors or agencies in relation to insects in general we are in a fair way to appreciate the nature of the origins and causes of insect outbreaks.

Climate affects insects, in general, by determining their geographical distribution, and, in particular, by regulating their rates of development and increase. The components of the climatic factor are temperature, humidity, and light.

Temperature affects insects by increasing or decreasing the rate of their metabolism. At low temperatures insects are less active, consume less food, moult less frequently, and grow more slowly. Below and above certain temperatures they cease to be active and become comatose, and extreme temperatures at either end

of the range cause death. This range varies from different kinds or species of insects, but in general it extends from 15° to 65° Centigrade. Sudden considerable changes in temperature may be fatal to insects, and Professor Bachmetjew has shown that insects are capable of surviving very low temperatures if these come on gradually or if thawing takes place gradually. An extreme fall of temperature, followed by a rise and then another fall, even although the second fall is less severe than the first, is almost always fatal. It is for this reason that insects, such as the common humble bee, can survive the extreme cold of winter, but frequently succumb to relatively mild spring frosts.

The temperature by regulating the rate of insect metabolism and development also regulates its rate of increase. Thus in the valleys of Switzerland the common cockchafer undergoes its development from the egg to the perfect insect in three years, but on the higher lands and foothills of the Alps it requires four or even five years. The reason is that the feeding and growing seasons are shorter at the lower temperatures of the highlands and the insect requires a longer period in which to attain full development. The effect of the longer period of development on the cockchafer's numbers is marked, for in warmer localities it is so numerous as to be a veritable pest, but in colder districts its numbers are so few that the damage it causes is negligible. An Austrian entomologist named Zweigelt has mapped out the distribution of the cockchafer in certain parts of Europe, and has shown that while in districts having a mean annual temperature of 7° C. and over, it is seriously harmful, in districts in which the temperature is below that figure it is negligible as a pest. In this country the chafer is most harmful in the South of England, but as we go north it becomes less common and less abundant, until north of the Forth it occurs only

rarely, and is of no importance as a pest of agriculture. As with the cockchafer, so with other insects, their occurrence and numerical abundance is regulated by the temperature.

Humidity or the amount of moisture in the atmosphere affects insects much in the same way as temperature, but its effects are less extreme and in practice, because it is almost impossible for changes in humidity to occur without a change in temperature following and *vice versa*, it is necessary to consider the two factors, temperature and humidity, together. In so far as it is possible to separate the two factors, it appears that very high or very low humidities, combined with high temperatures, are fatal to insects. At very low temperatures humidity is low because of the freezing of water, and it is difficult to decide which factor, low temperature or low humidity, is the more potent in affecting the insects studied.

At the same temperature certain humidities are more favourable to some insects than to others, and in general insects thrive best in atmospheres of moderately high humidity. The rate of growth of bacon beetle larvæ, for instance, may be three times as rapid in an atmosphere of 80 per cent. humidity as in an atmosphere of only 40 per cent. humidity.

The effect of light upon insect increase has been but little studied, and it seems probable that it is more important in deciding the habitat selected by the insect and so indirectly influencing its numbers than in affecting them directly. Many insects are negatively phototropic, shunning the light and living and thriving only in dark places, but the investigation of the effects of light on insects is difficult, partly because we have as yet no satisfactory method of recording variations of light intensity in the field, and partly because the reactions of many insects to light varies with the different phases of their development and with the sex of the individual.

Temperature and humidity acting directly on an insect constitute one of the most important factors governing its rate of increase and numbers, but the indirect effects of temperature and humidity are also important.

The effect of hot sun and dry weather in drying up the Blue-Bottles' food supply is just as potent a factor in retarding their increase as are the predators and parasites. So, too, such extremes of climate as droughts and floods, by killing the fine root hairs of plants, reduce their vitality, afford entrance for fungus diseases, and predispose the plants to attack by insects which are unable to attack the vigorous, healthy plants.

Drought and floods are now recognised as the frequent predisposing causes of outbreaks of many forest insects, such as the bark beetles and wood-boring beetles. In the London district in 1921 the drought, by lowering the vitality of the elm-trees, led to an epidemic of bark-beetle attacks, which in some of the public parks killed off many trees.

There is some evidence to show that climatic factors acting through the plant determine the production of winged forms of the greenfly or aphides living on the plant affected, and the indirect action of the climatic factors is almost as potent as their direct action on insects' increase.

The amount of food available to an insect is naturally a vital matter in relation to that insect's development and increase, and it is by increasing the food supply artificially that man himself creates the majority of his insect problems. The growing of crops in large but compact areas and the cultivation of pure crops of only one plant are wholly artificial phenomena. They afford the insect an uninterrupted and large supply of its host plant, and thereby favour its increase.

An insect living on wild Solanaceæ finds its host

plants scattered and mixed with plants which have no interest for it, but the same insect arriving in a potato field finds an unlimited and uninterrupted food supply. When its numbers increase, dispersal is no longer necessary to insure adequate feeding or breeding-ground. The risks which such a dispersal, necessary when the insect is living in a natural environment, entails are avoided in the potato field, and by the mere act of cultivating his crops as pure crops extending over large areas, man favours insect attacks on these crops. The extension of the cotton-growing belt in America resulted in an extension of the area of distribution of the cotton Boll Weevil, until that insect now extends over nearly half a continent, and it probably travelled largely by its own exertions through the ever-extending cotton-fields.

The storage of large quantities of such products as grain and timber in our wharves and warehouses is itself a direct cause of damage to these products by the insects which live in them. The menace of the grain weevils to our wheat stores in the war, a menace so alarming that it led to the appointment of a special committee of the Royal Society to consider and combat it, was the direct result of the concentration of the grain in large stores. The grain weevils found themselves with an unlimited supply of food and breeding-ground in which they could breed almost undisturbed. The docks and wharves at our ports constitute a constant breeding-ground for the insect pests of stored products simply because they afford a concentration of food material.

The extraordinary increase during the war of the louse, already mentioned, was the result of the concentration of large numbers of human beings in camps and barracks, combined with lack of adequate facilities for washing and for the practice of normal hygiene. In civil life the strongholds of the louse are overcrowded slums and "doss-houses."

By artificially increasing and storing their food supplies man is constantly favouring his insect enemies. Fortunately for him, there are other factors affecting their increase, and of these other factors the insects' natural enemies have of late years received special attention.

If we collect in the field any considerable number of caterpillars of some common moth and rear these in the house or the laboratory, we shall find that instead of rearing a moth for every caterpillar collected we shall rear only a proportion of moths, while in our breeding cages a number of other insects not knowingly introduced into them will appear. These are the two-winged *Tachinid* flies and the four-winged *Ichneumonid*, *Chalcid* or *Braconid* wasps. All are parasitic on the caterpillars, and their eggs or larvæ were present within or on the caterpillars when these were collected. Or it may happen that our caterpillars "wilt" and die off, and in such an event we are probably dealing with some bacterial, protozoal, or fungus disease.

These two groups of insect enemies, the parasites and epidemic diseases, are probably very important checks on insect increase. In the field we may observe many birds feeding on insects. The fly-catchers, the martins and swallows and the little tom-tits are known to most people as insect eaters. Then many mammals such as the mole, the shrews, and the hedgehog are known as insect eaters. So, too, are frogs, toads, lizards, and fishes. Spiders are largely insectivorous. Unfortunately our knowledge of the real part played by these groups in keeping insects in check is by no means precise. With regard to birds, despite the investigations of workers in America, on the Continent, and at home, we are still ignorant as to the insect food of birds, and all that can be said definitely at present is that during the nesting season many birds themselves consume, or feed to their nestlings, enormous

numbers of insects, and that fuller investigation of the food of nestling birds is much to be desired.

If our knowledge of the insect food of birds is deficient, that of the insect food of mammals, reptiles, batrachians, and fishes is even more meagre. It is even doubtful whether insects form an appreciable part of the food of some of those mammals which we call insectivores. As a zoological term in classification the name is useful, but as descriptive of the mammals' food it may almost be a misnomer. In this branch of natural history there is much work to be done. As Mr. Elton has so well pointed out in his charming and excellent book on *Animal Ecology*, accurate observations and proper recording of observations made in the field are still far too rare even among professed naturalists. With mammals, reptiles, batrachians, and fishes, as with birds, all we can say at present is that they play some part in checking insects, but to say how important that part is requires much fuller and more accurate investigation than has so far been given to the subject.

In point of numbers the insect enemies of insects are enormously in excess of the vertebrates, but in spite of this our knowledge of the relationship of predaceous and parasitic insects to their insect hosts is both fuller and more exact than our knowledge of birds and mammals which prey on insects; this, too, in spite of the minute size and concealed habits of parasitic insects. In fact, the subject has become so extensive and its study so specialised that it forms almost a distinct branch of economic entomology, and both in America and Europe special "parasite" research stations have been founded for its proper investigation.

A general account and discussion of insect predators and parasites has been given by Professor Balfour-Browne in his *Insects*, published in this library, and readers should refer to it. Meanwhile our concern is with the part played by insect parasites

and predators in checking or controlling outbreaks of injurious insects. In this regard the parasitic insects so far appear to be more important than the predators. While it is true that as a rule the individual predaceous insect destroys more insects than the individual parasites, the rate of reproduction and increase of these larger predators is as a rule slower than that of the parasitic insects and also than that of the host insect. The food of the predaceous insect is, too, more varied, and for this reason it is more difficult to assess the real value of the predator as a check on a particular pest. The tendency has been, therefore, to attach more importance to parasitic insects as checks on insect pests, and, because they are more numerous in species than the predators and more easily studied, we have more published information concerning them.

A parasitic insect may restrict itself to a particular species of host, or it may attack several species of host insects. In the first case it is said to be a specific parasite; in the second a polyphagous parasite. It may attack the host insect at only one stage in that creature's development, and so we recognise egg parasites, larval parasites, and pupal parasites. In one country or in certain circumstances a parasite may be an egg parasite; in another country or in different circumstances it may be a larval parasite. All these points have an important bearing on the relationship of parasitic insects to their hosts. It has been found, for example, that many insects are held in check only when the insects parasitic on all their stages of development are present. This is the basis of the American "parasite sequence" theory, which postulates that an injurious insect is kept under control only when all the parasites attacking each different stage of its development are present and active in the area or district affected. One most interesting aspect of this "parasite sequence" is that the sequence of parasites of the Gipsy moth, for example, comprises in Japan a

different series of parasites from the Gipsy moth sequence in Europe, while in the United States of America a third type of parasite sequence is evolving at the present time as a result of the introduction of Gipsy moth parasites there from Japan and from Europe.

If in any district or season the parasite sequence of some insect is for any reason incomplete, the result is the rapid increase in numbers of that insect. It may be that a parasite of the egg stage is not present in its usual numbers or is even altogether absent and that in consequence more of the host insects survive and reproduce, and a knowledge of the sequence of parasites of an injurious insect is essential to the proper understanding of its numerical status and potentiality.

Formerly it was considered that only the specific or monophagous parasites of an insect were effective in keeping its numbers in check. It was supposed that a parasite which had many hosts dissipated its energies and had no marked effect on the rate of increase of any of its hosts. This view is now recognised as a narrow if not an erroneous one. If a parasite is restricted to a single species of host insect, it is obviously dependent on that insect for its continued existence. If it killed out its host it would die out with it, and its only hope of survival must lie in some correlation between its rate of development and increase and that of its host. Its numbers as compared with those of its host may vary from year to year, but they can vary only within such narrow limits as will insure the survival of the host insect.

Much more interesting and more effective as regulating the numbers of an injurious insect are the polyphagous parasites, which attack and breed in more than one species of insect. These parasites may attack a wide range of hosts and they are for that reason more or less independent of any particular one of their hosts. Unfortunately we know as yet very little regarding their ecology. We know that in some

cases their presence and abundance in any locality vary with the richness of the insect fauna of the locality and that the insect fauna varies with the richness of the flora. In a few instances we can correlate their scarcity or abundance with the poverty or richness of the flora, but the study of the complete ecology of even one polyphagous parasite is a long business requiring several years for its completion. Meanwhile the important part played by the polyphagous parasites in regulating the number of an insect pest is being more fully recognised, and before long the ecology of at least some of the polyphagous parasites of such injurious insects as the Nun moth, the Spruce Budworm, the Oak Tortrix moth, and the Codling moth will probably be worked out fairly well. The ecology of these parasites is extraordinarily complex. Certain parasites of the Oak Tortrix moth—*Tortrix viridana*, for example—have as many as twelve alternate hosts, and these hosts feed on no less than twenty-three species of host plants ranging from such forest herbs as the wood sage (*Teucrium Scorodonia*) to shrubs like guelder rose and hawthorn and to trees like birch and sweet chestnut. The absence of any one of these host plants in a locality may therefore affect the numbers of the polyphagous parasite in that locality and through it the numbers of the Oak Tortrix moth.

It is known that variations in the composition of the forest flora affect the abundance of such forest pests as the Nun moth and the Spruce Budworm. In certain districts in Sweden, where because of the poorer soil the forests are composed of many small, slowly growing trees, the area and light available for other plants is limited, and in these districts the Nun moth is more plentiful than in other districts where the soil is richer, the trees are more widely spaced, and the forest flora is richer.

The comparative freedom of the western forest

areas of Canada from severe outbreaks of the Spruce Budworm has been ascribed to their richer composition. The western forests comprise many species of forest trees, hemlocks, cedars (not true cedars, but species of *Thuja*), balsam firs, and Douglas fir. So far they have been less ruthlessly exploited than the eastern forests, and these two factors, combined with higher rainfall, cause their flora to be more varied and richer than that of the eastern forests. In the east the forests, formerly consisting of pines, spruce, and balsam firs, were first reduced to forests of spruce and balsam because of the lumberman's exploitation of the pines, of which the white pine was the most valuable. Now the demand for spruce for paper pulp manufacture is rapidly reducing the spruce-balsam forests to forests of pure balsam. The balsam fir is probably the original host of the spruce budworm, and in any case it is the host which best suits that insect; and the higher the proportion of balsam fir in the forest, the higher the risk of spruce budworm outbreaks. Equally important, however, is the change in the flora which has taken, and is taking, place in the eastern Canadian forests. Just what the change is has not been adequately investigated, but there is little doubt that one of the parasites of the budworm, a braconid wasp of the genus *Phytodietus*, is adversely affected by that change, and until more detailed studies of the flora of these eastern forests have been made, the full extent of one of the main causes of budworm outbreaks cannot be properly assessed.

Apart from the question of the local flora and its effect on the parasites of any insect pest, yet another complication arises.

"Big fleas have little fleas upon their backs to bite 'em,

And little fleas have lesser fleas, and so *ad infinitum*,"

and parasites of insects also have their parasites, which we call hyper-parasites. These have also to be taken note of in our study of insect ecology. Moreover, an injurious insect may be attacked by more than one parasite at a time, and this super-parasitism, as it is called, has a marked effect on the fate both of the parasites and the insect pest. While in the year of its occurrence super-parasitism adversely affects the host insect, in subsequent years its effect may actually be to favour it by reducing the parasites' numbers. This happens when, because of the presence of the super-parasite, the first coming or primary parasite fails to reach maturity for lack of food, which it has to share with the super-parasite. Hyper-parasitism may be even more effective in favouring the host insects, and the phenomena of hyper-parasitism and super-parasitism are of the highest importance in relation to the rate of increase of an insect pest.

Because of the extraordinary complexity of insect ecology, we are still far from being able, except in rare instances, to assess which are the primary causes of insect outbreaks. We can, as the plant ecologists have done, classify the types of the main factors affecting the occurrence and prevalence of insects in any locality or environment. These factors are the same for insects as for plants—the climatic factor, the biotic factor (*e.g.*, predators and parasites) and the edaphic or soil factor. In entomology, however, the soil factor is less important than it is in botany, because its direct effects are limited and in general affect only such insects as live actually within the soil. On the other hand, the soil conditions, by acting through the host plant of the insect or, as we have seen, by affecting the actual composition of the insect fauna in a locality, are none the less an indirect factor of considerable weight. At present this study of insect ecology is still somewhat neglected by entomologists,

but it is gradually receiving attention, and one of the important advances recently made in the organisation of the Parasite Research Station of our Bureau of Entomology is the appointment of a plant ecologist who will be able to advise the Station on the botanical environment of any insect and assist in unravelling the many complexities which the proper study of an insect and its parasites present.

This closer linking up of entomology with botany is all to the good. As we shall see later, entomology is also linking up with chemistry and physics, and while the study of the insect as an insect must always be the basis of the entomologist's training and knowledge, narrow specialisation, formerly the chief barrier to the progress of economic entomology, is gradually giving way before the advance of a wider and more catholic study of insect biology and of the relationship of the insect to its environment.

Of the control of insect outbreaks by bacterial, protozoal, or fungus diseases our knowledge is still somewhat scanty. Various diseases which attack insects are known and have been and are being studied, but of the real part which they play in checking outbreaks of insects our knowledge is vague. Outbreaks of such insects as the locusts, the Nun moth and other Lepidoptera, the Sawflies, and certain weevils, are brought to an end by bacterial and fungus diseases; such half-domestic insects as the honey bee and the silkworm suffer from bacterial and protozoal diseases, but the extent to which such diseases occur in Nature is not readily determined, and until the bacteriologist, the protozoologist, and the mycologist specialise on insect diseases, knowledge of these is bound to be attained slowly. With the vast fields of medical and veterinary and plant pathology open to them, the mycologists, protozoologists, and bacteriologists are unlikely to devote their attention to insect pathology, which requires for its proper study a special technique and a

knowledge of insect physiology that even the entomologists themselves do not possess at present.

The major difficulty in the investigation of the relationship of insect diseases to the variation in an insect's numbers is that, while these diseases can readily be studied and the organisms causing them readily be cultivated in the laboratory, experimental work on a large scale in the field has so far resulted in failure. This has given rise to the opinion widely held by entomologists and by mycologists that insect diseases such as are caused by fungi cannot be used artificially to check insect outbreaks. That opinion is correct only in so far as our present knowledge of insect pathology can take us, but it really means that our knowledge of the technical methods of exploiting insect diseases is inadequate. Doubtless with increased knowledge of insect physiology and insect pathology the time will come when bacterial, protozoal, and fungus diseases of insects will be used in the control of insect outbreaks just as the parasitic insects are used to-day.

Meanwhile we know that various kinds of epidemic diseases exist among insects under natural or wild conditions and that they play a considerable part in regulating insect numbers.

CHAPTER IV

THE BIOLOGICAL BASIS OF INSECT CONTROL

ALTHOUGH a knowledge of the factors governing the increase of insects and the rise of insect outbreaks should form the basis of all measures designed to control or prevent the rise of outbreaks, in practice these

control measures are still applied on a more or less empirical basis. The reason for this is that in practice the need for some immediate remedy is usually too urgent to admit of a prolonged or systematic investigation of all the aspects of the outbreaks of the injurious insect responsible and that it is always difficult for the entomologist to secure financial support for the investigation of an insect when its injurious activities are in abeyance.

The result is that many of the control measures in use to-day are merely palliative measures originally designed to remedy matters during some exceptionally severe outbreak. Insecticides as a class are palliative measures bringing about a more or less rapid decrease of the insect during the first or second seasons of its abundance. Mechanical measures, such as fly-traps, grease bands placed round trees to entrap wingless moths or wandering caterpillars, or bait traps designed to attract moths, weevils, and "wireworms," are also still largely employed merely as palliative measures designed to secure relief during severe attacks.

More fundamental in their application are the control measures termed "cultural and parasite controls." Cultural measures are those which are brought into application by the modification of cultural practice, as when resistant or immune varieties or strains of a crop are substituted for less resistant varieties; or when the early or the late sowing of a crop is practised to evade the attacks of such insects as the turnip flea, beetles, and the frit fly of cereals. These are measures which may become part of routine practice and are more or less permanent in their effects. Parasite control is the term used to describe the breeding and release of the parasites of an insect pest in order to reduce its numbers more or less permanently. At present the use of parasite control is almost confined to insect pests which have been accidentally intro-

duced into a new area or country where, freed from their natural enemies which kept them down in their native land, they have become serious pests.

These two types of control measures—cultural and parasite—require, even for moderate success in application, a fuller knowledge of the ecology of the insect pest than do mechanical and chemical or physical control measures, and in particular the development and increased vogue of parasite control has called attention to the neglect of insect ecology in the application of control measures generally. For this reason we may consider parasite control first and see how a knowledge of the factors governing the increase in numbers of an insect is useful in that form of control and then how it may be equally useful in the application of other methods of control.

The control of an insect by breeding and setting free its parasites against it has in certain instances proved extraordinarily successful. In nearly all these instances, the insect to be controlled has been an introduced insect in the country concerned, and the causes of its undue abundance and increase have been an ample food supply, a favourable climate, and an almost total absence of its natural enemies. The food supply has been the staple crop or one of the staple crops of the country, and as a rule a crop which has been increasingly cultivated. For that reason no reduction in the food supply and breeding ground of the insect has been possible or even conceivable. The climatic factor is beyond man's control, and the obvious method of control, other than the use of insecticides, which the vast areas over which the insect attacks occurred precluded, has been that of introducing into the country a parasite or a predator, or several parasites and predators, which are known to attack the insect in its country, or countries, of origin. Briefly, the position has been that the insect has arrived in a new country leaving its natural

enemies behind, and the method of controlling it has been to send its enemies after it.

The most striking successes with this method are the control of the Cottony Cushion Scale in California by the introduction from Australia of the ladybird beetle *Novius* (*Vedalia*) *cardinalis*, and the control of the sugar-cane leaf-hopper and other insects in Hawaii by the introduction of various parasites and predators. These successes have created a vogue in parasite control, and nearly every country has now in its employ, or acting as collectors for it, entomologists skilled in the search for likely parasites of important insect pests. One of the functions of the Parasite Laboratory of the British Imperial Bureau of Entomology is to collect and rear parasites of insect pests required by the Dominions and Colonies, and although this station has been in existence only three years it has already despatched thousands of parasites and has difficulty in coping with the ever-increasing demand for more.

It must not be assumed that the collection and rearing of parasites for insect control is a relatively easy business. On the contrary, it is a much more complex task than even some entomologists realise, because so many different factors must be taken into consideration in deciding on what parasites to send, when best to send them, and how to send them. It must, in fact, be admitted that some of the early successes in parasite introduction were largely fortuitous, and we realise to-day that the chances of successful introduction are not always good, but that on the contrary failures must be frequent.

In the first place, before selecting a parasite to be sent to a new country it is necessary to insure that it is a parasite of the insect to be combated and not a hyper-parasite living on some primary parasite which has been overlooked. Again, it is essential to avoid sending out two parasites which may behave as super-

parasites and thus cancel one another out, so to speak. Then it is necessary to ascertain whether the parasite selected is likely to be attacked by hyper-parasites or be joined by super-parasites in the new country. This is information which is often most difficult to obtain.

Still other precautions must be taken, as, for instance, whether, in the new country, the parasite may not find some new host, quite other than its intended host—the pest—which it may prefer so well as to ignore the pest host altogether. It is also necessary to ascertain whether any insects other than the pest host may serve as alternate hosts for the introduced parasite and so enable it to carry on in times when the pest host is few in numbers. Sometimes, as we have seen, not one parasite or predator but a sequence or chain of them may be necessary to check same major pest, and here is yet another difficulty: to find, collect, and despatch such a sequence of natural enemies.

In the early parasite introductions many of these points were not recognised as vital for success, and even to-day are ignored in the hope that some of the parasites introduced may prove successful. In practical control work such "hit and miss" methods may be necessary where losses are serious and action is urgent, but the methods are not to be recommended. One grave danger of parasite or predator introduction is that the parasite or predator introduced may in the new country become injurious, either by becoming itself an enemy of the host crop or by becoming a hyper-parasite of some existing host parasite, and "hit and miss" methods of introduction allow of no safeguarding against these contingencies.

The complexity of the problems existing in successful parasite introduction are now recognised by the leading exponents of the method, and the days when the introduction of some parasite found by chance was considered satisfactory are over. The results of

parasite introduction, even when it appears successful, are receiving close scrutiny and, thanks to the work of such eminent experts in parasite control as Dr. W. R. Thompson, the head of the Farnham Royal Parasite Station, and of his former colleague and assistant, Dr. Parker, haphazard methods of parasite introduction and hasty optimism in assessing its results are now regarded with suspicion as unscientific and doubtfully valuable. Sound control work by the introduction of parasites is achieved only after patient and prolonged investigation of every aspect of the problems to be solved, and even when all the information so obtained enables the entomologist to select and secure the desirable parasite and promises reasonable hope of success there still remains the delicate and difficult matter of shipping or despatching the parasite or parasites selected and reared.

Obviously, the parasites must be shipped alive and must arrive in a healthy condition. They may be despatched to be released against the pest immediately on their arrival or they may be despatched in a stage where further rearing of them is necessary after their arrival. In some cases it may be necessary to keep the parasites in quarantine after their arrival in order to obtain definite information as to their behaviour in their new habitat. To insure success in parasite introduction every care must be taken to insure the well-being of the parasite during its voyage, on its arrival, and after its arrival. The conveyance of the parasites in cold storage affords a ready method of preventing the insects' development during the voyage, but at present we do not know enough about the effect of prolonged subjection to cold on insects to feel sure that this method is innocuous. Even if it be innocuous, the method has certain drawbacks, because it is not always possible to insure a gradual change from cold storage to normal temperatures on the arrival of the insect, and shocks such

as are produced by sudden changes of temperature may prove fatal. In the writer's experience, a batch of parasites was shipped in cold storage from London to Montreal and presumably reached that port safe and sound; from Montreal to Princeton, however, the batch was stored in a heated van, and it was no wonder that when the batch was examined the majority of the parasites were dead, and the rest died soon afterwards.

The study of this question of the shipment of parasites now forms quite a special part of the entomologist's work in a parasite laboratory or station, and soon we may hope to obtain safe and satisfactory methods of shipment applicable to different means of transport and transfer from cold to warm countries, and *vice versa*.

If despite all its difficulties the introduction of a parasite to a new area has been accomplished, the next question is to ascertain how far the parasite is effective in checking the insect pest. The usual test is to collect numbers of the pest insect in the year following the release of the parasite and for several years after. If the pest insects collected yield a number of parasites, and if in subsequent years this number becomes higher, then the parasite is said to be well established. Sometimes, however, the parasite may not be found or, in technical parlance, "recovered" for several years after its release. In this case its establishment is slow and doubtful. The "recovery" of the parasite is not always a criterion of success. Sometimes the parasite so laboriously introduced is already, unknown to the local entomologist, represented in the area by a few individuals. It has been related how in one instance a negligent laboratory assistant, having allowed a batch of newly arrived parasites to die, "released" their corpses. This satisfied his turbid conscience, but it led to an amusing error. The parasites were duly recorded as

"released." Next year they were recovered, and this so astonished the assistant that he confessed his negligence, and so enabled his chief to learn that the parasite he was trying to establish was already present on the area and that the supposed "recovered" parasites were really indigenous ones whose presence had been overlooked.

Accidents of this kind emphasise the need for very careful assessment of the actual status of the introduced parasite and of its effectiveness in control. A drop or decrease in the numbers of the insect pest or a marked reduction of its ravages may have no relationship at all to the introduced parasite. It may be that the weather conditions have checked the pest in its early stages or that some disease has attacked these. It may even be that for some reason still obscure the ratio of increase of the pest has fallen. Such a fall in rate of reproduction does take place in insects.

How, then, are we to assess the success of parasite introduction? Only by careful collection of the parasite by collecting and rearing numbers of the pest, and by keeping record of the numbers of the pest over a sample area of the crop or, better, over several sample areas or sample plots. By observations on these plots, carefully recorded, a fairly true account of the status of the pest and the parasite and of the relationship of the two can be obtained. When that has been done, and if the results are favourable, the "parasite introduction" is complete and has been successful. If the introduction has been successful and the numbers of the pest have fallen and keep falling, or remain low, over a period of years control has been attained.

The next thing is to estimate its value, having regard first to the loss prevented and second to the cost of applying the control. It is unfortunate that in Government departments and in most businesses the

accountants will insist in writing down the losses caused by insects for the year in which they occur, and will insist on charging to the same year's accounts the whole cost of control measures. The system is doubtless sound, but it is desperately unfair to the entomologist because the effect of it is to make his costs look absurdly high. Let us assume that the entomologist has successfully controlled a serious pest of an important crop. His experimental work, let us assume, has been done in one particular district and has extended over five years. Now to charge the cost of that work to that particular district and to the costs of these particular years is wrong, in that it produces a distorted account of the value of the work. It is time that Government departments and others judged scientific work by its value and not by its cost. However, the point to be emphasised is that successful control work done in one district will apply to all districts where similar conditions prevail, and not only to all districts but to all countries, and to assess its value on the basis of its cost is absurd. Such a principle is not applied in industrial chemistry or industrial engineering, but curiously enough, it is applied in industrial entomology. A chief reason for it is that the entomologist himself is rather shy of incurring costs, he has still some of the modesty of the shy be-spectacled butterfly hunter of the *Punch* cartoonist sticking to him, and is far too prone to be unduly pleased when the lay public or the administrative officials consent to view his collections or parade his laboratories.

In actual fact, the cost of equipping and maintaining an entomological station and staff is extraordinarily low compared with the cost of a chemical or physical or engineering laboratory, and the control of insect pests by means of parasites, as by other forms of biological control to be referred to later, is cheaper than to control them by the use of insecti-

cides, always assuming that the same standards of work and the same standards of assessment of results apply to both methods. We shall return to that point later, meanwhile it may be repeated that to judge the value of a new control method by its cost in one particular district is wrong, because the method once devised is available for all time and for all countries, and, always assuming that it is really effective, gives benefit, not for the year in which it is first applied, but for subsequent years also. On such a principle of assessment the control of insect pests by the method of parasite introduction is in certain definite circumstances a valuable and practicable method. The definite circumstances are that the insect pest in question is an introduced or exotic one, is comparatively free from parasites, and that the crop which it destroys is a staple and valuable one.

The control of injurious insects by their parasites under other circumstances has still to be tried out. By many entomologists it is considered that where an injurious insect is native in or indigeneous to a locality, and when it has a number of parasites attacking it, then the artificial encouragement of these parasites is impracticable. The contention is that the parasites are already pulling their full weight and any increase of their numbers by artificial means, such as the introduction of numbers of parasites from some other locality, can be only temporary in its effects. This contention is not easily refuted at present, because of the lack of accurate information, even in the case of our major pests, regarding the extent of their parasitisation from year to year and from district to district; regarding the relationship of weather conditions, first, to the pest itself and to its parasite and their effects on the relationship of the two insects; regarding the importance of variations in the flora, and other fauna of the locality, and finally, which is the more to be deplored, regarding the relationship

of agricultural or commercial practice to the pest and its parasite. It has been suggested that we do not even have actual data to support the hypothesis that the numbers of an insect and its parasites do bear any close relationship to one another. This last suggestion, it is only fair to say, has been put forward by one of the strongest and most authoritative advocates of parasite control, and rather with the intention of emphasising the need for acquiring information and data on these matters than with the intent to disparage the hypothesis.

At present the control of insects by encouraging their natural enemies in their native habitat has been practised only in the form of bird protection, and even this has been carried out more by bird lovers seeking some practical support for their hobby than by entomologists engaged in combating some particular insect pest. The encouragement of birds such as tits and warblers is undoubtedly to be approved by the entomologist, but the recently promulgated hypothesis of "territory" in bird life* raises the question as to how far the numbers of any bird species can be increased within a limited area. If the "territory" hypothesis means that each bird or pair of birds is jealous of its particular territory to the exclusion of others of its kindred, then evidently the increase in the numbers of these birds in a locality will be governed by the extent of the territory occupied by each pair and limited accordingly.

Further progress in the study of the relationship of birds to insect numbers is dependent as much on the ornithologist as on the entomologist, and will be most rapid when these two biologists co-operate. Meanwhile, the entomologist is more likely to advance his knowledge of the insect enemies of insects, and

* See Mr. E. M. Nicholson's volume *The Study of Birds*, in this Library.

the lines along which progress will be made are already fairly evident.

The steadily increasing value of our crops and stores, the tendency towards the cultivation of larger and larger areas of crops of one kind, the storage of larger masses of grain and other foodstuffs and of the raw materials of commerce, and the generally increasing interest of the public in insect problems, all favour the search for new and more enduring methods of checking losses caused by insects, and the success and romance of the control of insect pests attained notably by the Hawaiian sugar-cane growers has tended to call attention to the value of ecological work. Added to these factors is an increasing dissatisfaction with the empirical use of insecticides and a realisation of our present ignorance regarding their modes of action. Ecological work is therefore becoming more sure of sympathetic consideration and financial support by administrators and agriculturists alike.

In forest entomology, the ecological study of insects is already well advanced. The reasons for this are that cultural control measures, such as the rotation of crops, are not possible in forestry, because the crop takes at least thirty or forty years to mature and may take even a hundred years or more. The extent and height of the forest crop precludes the use of insecticides except when applied by aeroplane—a method still to be developed and perfected—and, finally, the forest entomologist has always been, since the days of Ratzeburg, the father of forest entomology, an enthusiastic field worker. Forest crops covering, as they do, large areas, offer more uniformly extensive habitats or biotic associations than do agricultural crops, habitats that change more slowly than those created or produced by agriculture and which therefore lend themselves more readily to study and classification. By the very nature of his work the

enthusiastic forest entomologist becomes ecologically minded. The long duration of the crop, the long-deferred financial returns, and even the awe and austerity of the forests themselves favour the longer view and the more philosophical outlook required for the study of fundamental principles. It is not surprising therefore to find that the best account of the principles of the biological control of insects is to be found in the literature of forest entomology, and that our outstanding European forest entomologist, Professor Escherich, of Munich, is a strong advocate of ecological investigation.

Briefly, the lines along which forest entomology is developing are the lines along which agricultural entomology will follow. An examination of recent forest entomological literature shows that more and more attention is being paid to the behaviour of insects in the field, and in particular to the causes of their variation or fluctuation in numbers. The effects of familiar forest operations—such as thinning—on the increase of insects are being studied, the effect which the removal of the brushwood or slash (tops and branches of felled trees too small or unshapely to be used as timber) has on bark beetle increase, the effect which vigorous growth has in causing trees to be more resistant to or better to recover from insect attacks are all subjects now being investigated. Wider problems, too, such as the value of mixed woods as compared with that of pure woods in reducing risk of insect outbreaks, and the value of natural regeneration as opposed to the artificial regeneration of woodlands, are being studied, and, as we have pointed out, the variation of the extent of parasitism and its relationship to the density and composition of the forest is also attracting attention.

In agricultural entomology ecological studies are being made of the insect fauna of the soil, and we may soon expect a study of hedgerow insects, but the

study of parasite control will, in agricultural entomology, probably begin in fruit farming and with a study of the parasite complex of some such insects as the Winter and Codling moths or in pastoral farming with a study of such an insect as the Grass moth (*Charaëa graminis*). In this work the foundations of a fuller understanding of the value of parasites as controlling factors will be obtained and the term "parasite control" will no longer be restricted in practice to the somewhat special use of parasites against exotic insects only.

The fact is that an understanding of the ecology of an insect pest is really necessary in applying all types of control methods. For generations the use of bait traps consisting of pine logs or pine bark has been practiced against one of the most important insect enemies of re-afforestation, but it is only within recent years that their use has been completely justified as a result of long-range ecological work.

The Large Pine Weevil (*Hylobius abietis*) is known to the forester as the worst enemy of his young pine plantations, established to replace the crop just felled. In the older pine woods the weevil, a small beetle with a longish snout, is quite innocuous. It feeds in the tops and branches of the trees, causing no appreciable harm, and breeds in the roots of dead or dying trees or in branches broken off by snowstorms or wind, and in the stumps and roots left by the forester when thinning his woods.

Forests are always planted densely in order to cause the trees to grow up to the light with few branches, and consequently as the more vigorous trees crowd out and suppress the less vigorous these poorer trees are removed as "thinnings." Now it can be shown that after a thinning has taken place the numbers of the weevils in a wood or forest plot increase in numbers because of the increased breeding ground afforded by the stumps of the thinned-

out trees. So, too, when the forest becomes mature and is "clear felled" all the trees are removed and their stumps afford abundant breeding ground for the weevil. Meanwhile the forester replants the area and thus provides the weevil with a supply of tender trees eminently suitable as food. The weevil is then in an ideal position with food for its grubs in every stump and for itself in every young tree or "plant." As it increases in numbers it soon devours the bark and buds of the young trees and in many instances felled pine areas in this country have been re-planted as many as three and four times because of the depredations of *Hyllobius*.

The measures taken by the forester to control the weevil are various and are also of varying value. Until recently all of them were devised on the assumption that the place and time to control the weevil were after felling in the felled area itself. Many of the measures practised were of very little value, as, for instance, the painting of the stumps above ground with creosote to prevent the weevils from laying their eggs in them. That measure was useless because the weevil always lays its eggs in portions of the stumps below soil level. Another worthless measure was the spraying of the young plants with poisons such as lead arsenate. That measure is useless because the weevils do not eat the outer bark of the twigs or stems of the young trees, but reject that bark and gnaw through and under it to the tender green cambium below, which is not reached by the arsenic spray. Professor Escherich suggests that the weevil is immune to poisoning by arsenic, but there is reason to doubt his suggestion.

A more useful measure against the large pine weevil is the use of heaps of fresh pine sawdust or of freshly peeled pine bark or freshly cut pieces of pine branches to attract the weevil, which come in numbers to these bait traps and are then collected

and destroyed. This method is a time-honoured one, and is, despite its simplicity, the best and cheapest method of control. The only defect in its use was that it was applied at the wrong time. The large pine weevil is always present in our pine woods, usually in small numbers, and it is only when its breeding ground is increased by felling operations that it ever attains sufficient numbers to become injurious.

If the forester traps it before he begins felling, as he can easily do, then he can reduce its small numbers still further, and, indeed, to such small numbers that even when felling does take place some years must elapse before the few weevils left after trapping can rear sufficient offspring to cause any serious injury. This method of early trapping in the woods before they are felled has been recently tested by experiment with highly satisfactory results. It has the advantage that it actually prevents weevil outbreaks at much less cost than the older system of trapping after felling, which was, too, merely a palliative measure. The period during which the stumps on a felled area remain attractive and suitable to the weevil varies with the locality, but in the dry, warm climate of the south it lasts only three years, and in the wetter, colder climate of the North it lasts about four years. By early trapping of the weevil the forester can so reduce its numbers that the stumps cease to be attractive to the weevil before it has had time to increase sufficiently to become a menace to replanting.

This method of control has been based on a detailed study of the weevil and its relationship to forest practice, but some ten years were occupied in completing the work. All the commonly practised control methods were tested experimentally, the parasites of the weevil were studied, parasite control was tried, but after piecing together all the information obtained from these experiments and from observa-

tions carried out in different localities at intervals during ten years, it became evident that the only sound control method was that of trapping in the woods to be felled, a year or two before the felling was to take place.

This work on the control of the pine weevil was carried out by H.M. Forestry Commission. The experimental work was done in two of their forest "Divisions," but its results are applicable throughout the country, and even to another species of *Hylobius*, *Hylobius pales*, occurring in the eastern United States, and although the work was slow the value of it is not to be measured by its cost. In this particular case the cause of the outbreak is increased food supply, and the best control measure applicable is to trap the insect before the increase of food supply is brought about and so prevent the weevil from gaining advantage of it. It should be pointed out that the method is dependent for success on the co-operation of the forester, and that it is applicable only where forestry practice is well organised and properly planned.

The principle of preventing insect outbreaks by anticipating the operations of the forester or farmer or merchant is still too little employed in entomology to-day. It is, however, a principle which will become more and more applied, and it is especially applicable to the control of insects whose increase is governed mainly by the food-supply factor. Its application depends, however, on the fullest knowledge of the insect's ecology, and in particular on a knowledge of the relationship of the insect to the methods and practices employed in the industry affected. In the investigation of the insects injurious to stored products, such as cacao, spices, and dried fruits, which is being undertaken by the Entomology Department of the Imperial College of Science and Technology, the progress so far made indicates that in the control

of insects in stores and warehouses a wide knowledge of the ecology of these insects will form the only sound basis. In the cacao industry, for example, it is evident that no real improvement in the condition of imported cacao can be looked for until a full ecological study of the Cacao moth (*Ephestia elutella*) has been made, both in the cacao growing countries—such as West Africa—and in our ports at home. Undoubtedly the insect infestation arises because of the accumulation of quantities of cacao, but just when infestation begins, whether after fermentation of the cacao or before that operation, is uncertain. The effect of the presence of mould in the cacao appears also to have some bearing on the extent to which cacao is attacked by the *Ephestia*, and in the case of nearly all stored products there is evidently a correlation between the condition of the products and the degree of insect infestation.

One of the results of the investigation of stored products insects—including insects infesting timber—is to show how very meagre is our knowledge of the real food of insects. As Mr. Uvarov has pointed out in his summary on Insect Metabolism, recently published in the *Transactions of the Entomological Society*, we know very little concerning the chemical composition of the food of insects, and less still of the physiology of their digestion of it. The organised control of insects injurious to stored products will depend on the acquisition of a fuller knowledge of their feeding habits. Meanwhile it may be repeated that many of our stored products pests are scavenging insects, which under natural conditions feed on moulds and the products of decay, and that the first step towards their control is to insure freshness and cleanliness in our stores. Better hygiene combined with the judicious and timely use of chemical and physical control measures are at present the best methods of reducing outbreaks of insects in our

stores of food and the raw materials of industry. The two measures must go together, however, for chemical or physical control measures of themselves are merely palliatives, and our hygienic measures are still limited in their effects pending a fuller knowledge of the insects' ecology.

In the control of stored products insects, success will depend very largely on the co-operation of the producers in our Colonies and of the importers and merchants at home, and one of the most interesting parts of the writer's work in directing the stored products research at the Imperial College is that which is concerned with trying to form a liaison between the Colonial producers and Government officials and the wharfingers, merchants, and manufacturers at home. It is also extremely interesting to find that in England we can carry out research on such insects as the Cacao moth, the Nutmeg weevil (*Aræcerus fasciculatus*) and the dried fruit moth (*Plodia interpunctella*) which is both interesting and helpful to our colleagues in West Africa, Trinidad, and Australia. For example, one of the needs of the Gold Coast authorities in their work on the improvement of cacao marketing was a knowledge of the insect conditions prevailing in their cacao on its arrival at our home ports. This we have been able to supply, and in return have been able to secure an exchange of programmes of investigation so that part of our investigations at home run on parallel lines with the work on the Gold Coast. The result is that a full knowledge of the ecology of the insect pests of cacao may soon be hoped for, and that when control measures come to be devised they will have for their basis a real understanding of the problem as it appears in the cacao growing country and at home, and an understanding of the difficulties of all the parties concerned in the cacao trade. This very desirable consummation of the work, when it is achieved, will

have been possible because of the ecological work done. It is no exaggeration to say that in all economic entomology problems the best hope of a solution lies, not in the indiscriminate and hasty resort to the use of insecticides, but in the frank and open investigation of all the aspects of the problem with the object of placing any control measures devised on a broad and sound basis.

The use of insecticides and of heat and cold in the control of insects has an important place of its own in economic entomology, but the basis of all control measures ought to be a thorough study of the biology and ecology of the insect concerned. Even in the use of insecticides and of physical control measures much can be gained from a knowledge of the biology of the insect, and we may now consider these chemical and physical methods in some detail.

CHAPTER V

THE CONTROL OF INSECTS BY CHEMICAL AND PHYSICAL MEANS

THE use of poisonous chemicals and of high and low temperatures for the destruction of noxious insects is a very old practice and is still the most popular and most generally employed destructive measure. In its application there is, however, one serious limitation—namely, that the chemical or physical means used should kill the insect without having any deleterious effect on its food or surroundings. Obviously, one would not try to destroy insects on one's potato patch with a chemical which would also destroy the potatoes. This limitation of the chemical substances

or physical means to be used is an extremely important one which affects the whole question of control by chemical and physical measures. In the first place, because one cannot readily submit plant feeding insects to fatally high or low temperatures—lethal temperatures as they are termed—without at the same time submitting the plants to these temperatures, the use of this control method is practically ruled out against pests of agricultural crops. Accordingly, in agricultural entomology, chemical means only are used at present, and in general they are spoken of as insecticides.

The use of any chemical or chemicals as an insecticide is limited in agriculture by its effect on the crop and in industry by its effect on the product. For this reason and because substances useful as insecticides in agriculture—*e.g.*, coal tar products as winter washes are not applicable in industry and *vice versa*, it is advisable to consider these two branches of entomology separately. In actual practice the study of insecticides for use on growing crops is quite a distinct branch of entomological chemistry from the study of insecticides for use on stored products.

The agricultural entomologist recognises two classes of insecticides, which he terms stomach poisons and contact poisons. The first class are the insecticides which are believed to act when they have been eaten by the insect and have entered its stomach. The second class are the insecticides which are presumed to act merely by touching or making contact with the insect's integument—or "skin"—or by entering its respiratory system through the little openings or spiracles which open on the sides of its body. Whether this classification is really scientific is doubtful, but it is useful inasmuch that stomach poisons can be used only against insects which gnaw solid food and are of no value against insects which suck the sap or juices of plants by piercing them. Thus we may

say that in general stomach poisons are used against the "biting insects"—such as locusts, caterpillars, leaf-eating beetles, and weevils—and contact poisons are used against the "sucking insects"—such as green-fly, plant bugs, and scale insects. Contact insecticides do, of course, act on biting insects and are used against them, but their particular use is for the destruction of the sucking insects.

Stomach insecticides are usually applied in two forms: as liquids containing poisonous salts—such as arsenical compounds in suspension—and as dusts consisting of poisonous salts in admixture with some dry substance—such as chalk or kieselguhr—which helps in the "spreading" and adhesion of the dust and reduces the danger of wetting.

The chemical substances suitable as stomach insecticides are rather limited in number, and, in fact, arsenical compounds are in practice the most generally useful. They have the desirable attributes that they are not water-soluble and are, therefore, not washed off the plants by rain, that they are relatively cheap, and that they are easily procured. They are, too, relatively highly toxic. Within recent years arsenical dusts have been preferred to liquid arsenicals, and with the development of aeroplane dusting it seems likely that they will gradually replace liquid arsenicals. Arsenic compounds are also used in the making of poison baits which are employed against such insects as locusts and cutworms and consist of bran and poison moistened with water, with or without the addition of treacle or molasses or of bundles of herbage dipped in strong arsenic "solution."

The purpose of the stomach insecticide is to cover the plants to be protected with a fine coating of arsenic so that in feeding the insect absorbs or swallows the arsenic with its food. To insure a general distribution of the arsenic over the plant the insecticide is applied as a very fine spray or mist. The

objections to arsenical compounds as insecticides are that their careless use may result in "scorching" of the plants sprayed—this happens when water-soluble arsenic is present in the spray used—that they are highly poisonous to man and other animals, and that they are rapidly increasing in price.

Apart from arsenical salts the chief inorganic salts used as stomach poisons are copper sulphate—the basis of Bordeaux mixture—and the fluorides and fluosilicates of sodium.

The contact insecticides offer a much wider range of substances than the stomach poisons, and within recent years the investigation of possible substances for use as contact insecticides has almost revolutionised the use of insecticides, so that to-day the entomologist who would keep abreast of new knowledge must be prepared to undertake the serious study of organic chemistry. The most important contributions to our knowledge of contact insecticides have been made by the Insecticides Department of the Rothamsted Agricultural Experiment Station, at Harpenden, under the leadership of Dr. Tattersfield. The results of his work are of too technical a nature to be described here, but one very important general result of it has been to raise the standard of all insecticide work and the standard of tests of the efficiency of insecticides.

In general, the progress recently made in the investigation of contact insecticides has been to direct attention to organic compounds, particularly derivatives of shale and coal-tar oils, and to the toxic extracts of such plants as *Tephrosia*, *Deguelia*, and *Chrysanthemum*. It seems, in fact, that pyrethrum extracts derived from species of *Chrysanthemum* may yet prove the most toxic of insect poisons, and that their use may be greatly extended. Pyrethrum powder, derived from the dried and powdered flowers of *Chrysanthemum*, has long been used as an insect powder, but until recently the true chemical nature of

the toxic principle it contained was not certainly known.*

In Germany and in Holland an investigation of the so-called tar distillates—oils distilled from coal-tar—has led to a very important extension of the use of the substances in the control of fruit insects by applying them as winter washes when the trees are dormant.

In general, shale and coal-tar oils, plant poisons like pyrethrum, and sulphur compounds, afford the most promising sources of contact insecticides, and with the extension of these sources there has also developed a much more accurate chemical knowledge of how insecticides act and why they act. This will doubtless soon be followed by a better knowledge of the physiology of insecticides, and the control of insects by insecticides will be placed on a rational, scientific basis. Such a development is highly to be desired in order to check the shameless exploitation of the anxious crop grower by firms whose sole interest in selling their "insecticides" is to derive revenue from some by-product of their manufacture, the value of which as an insecticide has often never even been tested and is assumed to exist only because the by-product is evil smelling or contains some form of cresol. It is no test of an insecticide to immerse insects in it. The real test of an insecticide is its capacity to reach, penetrate, and to kill the insect in its normal habitat, and this is no easy matter.

One point to be noted with regard to the use of insecticides in agriculture is that as a rule their effect is immediate, and there is no great demand for an insecticide which shall be lasting in its effects.

In industrial entomology the control of insects by insecticides and by their submission to extremes of

* Some of the most efficient "fly-killers" consist of a combination of a heavy paraffin and pyrethrum extract.

heat and cold are almost the only measures available against them at present, but even so the use of these measures is still largely haphazard and unscientific. In the choice of insecticides, among which poisonous gases are the most generally used, the same limitations occur as in the application of insecticides to plants. Any substance used must not be deleterious to the product treated, and in fumigation by hydrocyanic acid gas, for example, the greatest care is necessary to insure that no harmful effect results. This gas is absorbed and retained by different products in different degrees. Thus, while cacao beans will absorb only thirteen parts of the acid per million by weight, the same beans if crushed to powder will absorb as much as sixty-three parts per million. Some products rich in essential oils—such as cloves and other spices—cannot be fumigated because they absorb so much of the gas.

Hydrocyanic acid, because of its rapidly toxic effect on insects and of its easy preparation and application and relatively high penetrating power, is one of the most useful insecticides for use in commerce, but at present its use is seriously limited because of the very variable absorption of the gas by different products. Not only is the gas absorbed, but it is held or retained, and such products as dried fruits may retain appreciable quantities of hydrocyanic acid for many weeks after fumigation has been done.

Another very useful fumigant, carbon bisulphide, is limited in use because it is highly inflammable, and many otherwise useful sprays consisting of heavy paraffin oils and pyrethrum extract are limited in use for the same reason.

The use of extremes of heat and cold in stored products entomology is not so frequent or so general as the use of insecticides. In the United States, as Professor Chapman informed the writer, some flour millers raise the temperatures of their mills and ware-

houses during the week-end to eliminate such insects as the meal moth (*Ephestia kühniella*) and the grain weevils *Calandra* and *Sitophilus*. In the timber industry the sterilisation of oak and ash timbers infested by *Lyctus* beetles and by long-horned beetles, especially the so-called "red-headed ash borer" (*Neoclytus erythrocephalus*) is becoming a general practice in the United States, and is now practised by the more enterprising timber importers and merchants in Britain. The method was devised by Messrs. Craighead and Snyder, two leading American forest entomologists, and in its present form is practised in conjunction with the kiln method of seasoning timber. The exposure of insect-infested timber in a steam kiln to a temperature of 130° Fahrenheit at a humidity of 100 per cent. for three or four hours is sufficient to sterilise it. Experimental work to improve this method, and, if possible, to reduce the degree of temperature which is higher than is desirable for seasoning purposes, is in progress at the Forest Products Research Laboratory of the Scientific and Industrial Research Department at Princes Risborough.

The use of very low temperatures to check insect infestation of stored products is not yet in general use. At the Imperial College experimental work on the freezing of insects infesting almonds and nuts is in progress, and it seems that the method has distinct possibilities commercially. The method tried was double freezing—that is, the freezing of the insects for some hours, then submitting them to a warm temperature for a short period, and finally freezing them again.

The defect of all these methods of control against insects in stored products is that, while they get rid of the insects for a time, they do not prevent re-infestation. This is a defect which also exists in the application of insecticides in agriculture, but because the crop is only a short time on the ground, except in

fruit farming, the temporary nature of the effects of insecticides is less of a drawback than in commercial entomology.

Obviously, insecticides and sterilisation by heat and cold must be supplemented by other measures, and in commercial, as in agricultural and forest entomology, we are once more forced to face the study of commercial entomology on a fundamental basis. In this more scientific investigation there are two main lines of work to be followed. The first is to study closely all the conditions or factors which contribute to the increase and continued occurrence of insect infestation. The second line of study is to investigate further the use and application of insecticides and physical destructive agents from a bio-chemical and bio-physical standpoint.

In the first line of study the co-operation and goodwill of all the parties engaged in the particular branch of trade or commerce is essential. One of the most difficult and least pleasant duties which the commercial entomologist is called on to perform is to decide in some dispute regarding damage resulting from insect infestation which party is responsible, and in nearly every instance it is evident that all parties are to some extent responsible, because all of them have contributed to the favouring of infestation. One case which occurred some years ago in the timber trade will serve to illustrate this and serve to indicate the nature of commercial entomological problems in general. The case began with a request for advice regarding the identity of some grubs which were destroying the fittings and furnishings of a small liner. The grubs were identified as those of one of the powder post beetles (*Lyctus brunneus*) and, in response to further inquiry, it was reported that the presence of the insect was due to the use of American oak, for the fittings and furnishings, which contained a high percentage of sap-wood. On the strength of this in-

formation the owners charged the shipbuilders with responsibility for the destruction. Then came a request from the shipbuilders for advice, which resulted in their approaching the timber merchant and importer. He, too, came for advice, and it may be noted that all three parties were acting quite independently in this regard, and that none of them knew the source of the other's information. Finally, it became impossible for the writer to conceal from the three parties that each was consulting him, and they were advised to settle the matter among themselves, and each to bear part of the loss. The reasons for this were that while the timber importer had infested stocks of American oak in his yard, so too had the shipbuilder stocks which had not been obtained from this particular importer. The shipowners also had certain furnishings, not supplied by the shipbuilder concerned, which harboured the *Lyctus* and, with the infestation so far advanced, it was literally impossible to allocate original responsibility. The parties were advised of this position, and, realising that at law the case would be decided on other than strictly scientific grounds, they settled it out of court.

One of the difficulties which retard the prevention and control of insect infestation in commercial products is the very natural desire of the parties suffering to place the responsibility on somebody else. This, coupled with the desire and need for secrecy resulting from competition in business, makes the acquisition of accurate information regarding the real origin and extent of infestation very difficult and usually impossible until all the parties find themselves sufficiently hard hit to make it worth their while to face their difficulties frankly and in conjunction with one another. So great sometimes is the desire to conceal the occurrence of insect infestation that on one occasion recently one party destroyed part of a consignment of goods rather than risk marketing it and

so letting its rivals in the trade know that their goods were sometimes infested.

As we pointed out, however, in referring to the losses caused by insects, this hesitation on the part of commercial firms to face the facts of insect infestation of their wares is gradually disappearing, and instead of trying to saddle their colleagues in trade with responsibility all parties are beginning to realise that only by a combined effort can their problems be solved. In Germany there has been recently formed a laboratory for the study of stored products infestation, which is supported and financed by commercial interests. In England research in stored products entomology is still dependent on Government support, but there are reasons to hope that soon commerce itself will contribute towards the work.

On the bio-chemical and bio-physical side the work on the prevention or reduction of insect infestation is concerned mainly with the improvement of the insecticides now in use—for example, in the application of hydrocyanic acid gas, and in the investigation of the action of insecticides and temperature both on the insects and on the products. The Ministry of Health has, naturally, an interest in this work, but it is to be wished that their attitude towards the sterilisation of foodstuffs by insecticides was less negative and more positive. For example, a definite pronouncement by the Ministry of Health as to what degree of absorption of hydrocyanic acid (prussic acid) by food products is safe would greatly help both the entomologist and commercial interests, and a more active policy in the direction of a sterner restriction of the marketing of infested foodstuffs would also benefit both the trade and the public. This raises the question of legislation as a means of insect control.

CHAPTER VI

*LEGISLATION AS A CONTROL MEASURE
AGAINST INSECTS*

It may seem absurd to consider the suppression of insects by law. One does not hope to prevent the ubiquitous house-fly from disturbing a post-prandial "forty winks" by threatening the law against it. Nevertheless, legislation directed against the spread of injurious insects exists and is one of the most difficult and least grateful branches of economic entomology.

In general, legislation is directed mainly against the introduction into a country or state of injurious insects from other countries or states or against the spread or dispersal of some injurious insect within a country. As a rule the insects "scheduled" are pests of important staple crops, and legislation is concerned mainly with insects attacking plants and with the prevention of the ingress of injurious insects on imported plants or plant products. Sometimes the measures are directed against a particular insect, as when our Ministry of Agriculture restricts the importation of potatoes from certain countries or districts of a country to prevent the entry of the Colorado beetle, or the importation of cherries to prevent the entry of the cherry-fly. These special measures are, however, emergency measures and as a rule legislation aims at the more general policy of preventing the entry of injurious insects on their host plants. In the United States more drastic measures are taken than in any other country, and the legislation embodied in what is known as "Quarantine 37" amounts almost to the total prohibition of plant imports. As a result, in Europe, and particularly by Holland, this plant quarantine

Act is regarded as an abuse of entomological legislation by political and commercial interests.

The prime defect of all legislative measures is that they may be abused, and while drastic legislative measures to prevent the introduction of a serious pest into a country may at times be necessary, such measures should be regarded as emergency measures and removed as soon as the danger is over.

In England legislation against the introduction of injurious pests is enacted through the Diseases and Insect Pests Acts, which are administered by the Ministry of Agriculture and Fisheries and, in so far as pests of forest trees are concerned, by the Forestry Commission in consultation with the Ministry. At present it consists in the restriction of the importation into England of all nursery stock (or young plants) from countries other than Scotland, Ireland, and the Channel Islands, which is not accompanied by a certificate that such stock is free from certain insects, such as the Cherry and Apple Fruit flies, the Potato moth, Capsid bugs of apple and the Colorado beetle. The list of pests named in the Diseases and Insect Pests Acts are known as "scheduled pests," and any nurseryman or private individual finding a scheduled pest on his premises is required to notify the fact to the nearest police station, which then informs the Ministry of Agriculture. On receiving such a notification, the Ministry has powers to visit and inspect the premises and to restrict the removal of the infested plants or of any plants from the premises or to order their destruction. In addition the Ministry has a staff of inspectors at our ports, whose duty it is to inspect consignments of imported plants for insect pests and fungus diseases.

This system of legislation works fairly smoothly, is apparently effective, and is relatively easily modified to suit special emergencies. Thus the Ministry can at any time cancel an existing D.I.P. Order, as it is

called, and modify it or issue a new one. The system is not unduly irritating to our foreign customers and puts them on their honour, rather than antagonises them, by accepting the certificates of their own plant protection services as a guarantee of clean stock. It is, in fact, based on the only rational basis of insect legislation—the reliance on the entomologists and mycologists who compose the plant protection services of the country concerned. The ways in which an insect may enter a country are so numerous and so varied that it is really impossible to insure absolute protection against its introduction. Even the drastic quarantine system of the United States cannot insure complete elimination of the risk of injurious insect introduction, and, that being so, the less irritation and the less antagonism set up by legislation, the better. Moreover, when, as we must frankly admit, the complete prevention of the entry of injurious insects is impossible, it is evident that the best safeguard against their spreading and causing devastation is to have an efficient staff of entomologists always on the lookout for them. The more efficient and the better equipped that staff is, the greater the protection.

In this country we take at present no steps to prevent the introduction of injurious insects in imported products other than plants. We have suffered recently from an invasion of powder post beetles in imported timber from the United States, and the question of legislation to check that invasion has been raised in commercial circles. Unfortunately any legislation now will not much remedy matters, because these beetles are established in almost every yard and workshop in the country which uses oak and ash timber. Moreover, the remedy lies rather in the hands of the timber trade, which can protest, and is, in fact, protesting, to the American trade and can back up its protests by cutting down prices. The Forest Products Research Laboratory at Princes Risborough is, however, collect-

ing data and statistics regarding the extent to which American timber arrives at our ports infested by *Lyctus* beetles, and there is no doubt that when these figures are available a satisfactory reply from the United States timber trade will be forthcoming without recourse to legislation.

Legislation is a necessary evil; alone it is ineffective in excluding injurious insects, but combined with an efficient entomological service it can serve a useful purpose. In fact, with legislation, as with all methods of insect control, efficiency depends far more on the entomologist and on his knowledge and tact than on any form of words or composition of an insecticide.

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PARASITES

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PARASITES

CHAPTER I

DEFINITION OF THE PARASITE

THE following pages will not attempt to give a detailed account of parasites. For that a separate volume would be required, or more than one. We shall be wiser to select from the great mass of facts known about parasites and to emphasise those which best illustrate the main principles of *Parasitology*. We have to try to understand the way of life called *Parasitism*, a way of life which has been adopted, in response to those influences which have determined the evolution of species in general, by many animals and some plants. We also have to study the effects of this way of living, both upon the parasites themselves and upon those other animals and plants upon which the parasites prey and which are naïvely called their hosts. We shall learn by doing this something of the great importance of parasitology to man, not only because he is himself the host of many parasites, some of which cause in him serious disease, but also because his domesticated animals and crops and food supplies and manufactured goods and buildings and other works of his hand are damaged by them.

But before we can understand properly the parasite's way of living, we must first very briefly inquire how life maintains itself upon the earth. How it arose in the beginning of things we do not know. All we can say with honesty is that life seems to have

originated from some kind of dead elementary protein that acquired the power of movement, of feeding itself upon simple chemical stuffs which perhaps were allied to itself, of growth, of sensitivity to external influences and the power to adapt itself to these incessant stimuli from its environment. Most important to its subsequent evolution, it also acquired the ability to reproduce its kind and to pass on to its offspring something of its own nature.

From such elementary life all the living things of to-day are descended; and at a very early stage in their development two methods of feeding were distinguished. One of these was practised by the creatures which gave origin to all the plants, the other by those from which the animals have been derived. The difference between them can be broadly summarised.

The plants have retained the power, theoretically ascribed also to the earliest living jelly, of feeding upon simple chemical compounds. They possess a green pigment called chlorophyll, or other pigments allied to it (see *An Introduction to Biology* in this series), which enable them to split up the carbon dioxide of the air in the presence of sunlight, the carbon being retained and built up into sugars and starches, the oxygen being set free. They can also take the nitrogen they need for building up the proteins of their protoplasm from such simple compounds as the nitrates in solution in water, and some of them can even utilise the nitrogen of the air.

Along another line developed organisms which have no chlorophyll or allied pigment. They could not, therefore, perform these remarkable feats. These are the animals. They cannot assimilate carbon in a form less complex than such carbohydrates as the sugars and starches or hydrocarbons like the fats; nitrogen they must obtain in the relatively complex form of proteins. All these substances must be split up into simpler compounds before they can be used in their

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bodies, and this is done by ferments made by the animals themselves. To carry out this relatively elaborate process the animals need a digestive system. Since the proteins and carbohydrates and fats are only to be found in the bodies of other animals or plants, these must be sought out, chased and perhaps fought before they can be consumed. The animal, therefore, needs also locomotor organs and weapons of offence and defence, as well as muscles to move it about and a nervous system to relate the whole animal as a unit to its surroundings and to control its activities. The plant need not move about from place to place, nor does it require a digestive tract or a nervous system. To this fundamental difference in the mode of feeding, therefore, a great many of the differences between the plants and animals can be traced. The plant's way of feeding is called holophytic, the animal's holozoic; and although there are some plants like the pitcher plant and the sundew, which feed like animals, catching live insects and secreting ferments which digest them, and some animals, especially among the primitive ones, which, like *Euglena*, for instance, contain chlorophyll, and can live either holozoically or holophytically, the general distinction does hold true and those exceptions which occur prove the rule.

All living things, however, are not either holophytic or holozoic. Some there are, both animals and plants, which live in the juices of other animals and plants that are dead and decaying. Lying there in a bath of dead liquid organic matter, they absorb it directly through their permeable skins and use it as food. Such creatures are said to be saprobiotic; and if they belong to the animal series they are called saprozoic, if to the plant series, saprophytic. Many parasites are saprobiotic in the juices of their living hosts, and some of them have arisen from true saprozoites and saprophytes that live in dead liquid organic matter in the outer world.

In our ponds and ditches, for example, where vegetable matter is decaying, we find those minute lowly lumps of primitive jelly called amœbæ. Living in the intestine of frogs that delight in such ponds, we find other amœbæ; and we may suppose that these have been derived from ancestors which once lived, ages ago, a free life in the pond. But some of them entered the frog either through its mouth or through its vent and, slowly becoming accustomed to life in the intestine, finally adopted that way of living. Probably *Entamœba coli*, which lives in the intestine of almost every human being alive, arrived there in a similar way, long ages ago, when the ancestors of man were less fastidious about contact with decay and putrefaction than most modern men are.

Neither *Entamœba coli* nor the amœbæ in the frog's intestine is strictly a parasite, but they indicate without doubt one way in which the parasitic habit may arise. They are instances of the kind of association between animals, or between animals and plants, that is called symbiosis, a term which means association for mutual benefit. Another example of it is the little tubular green *Hydra* with its circlet of tentacles, that lives in our freshwater ponds and streams. At first sight this creature seems to be a contradiction of the distinction given above between the animals and plants. It gobbles water-fleas by the dozen and is obviously an animal; yet its tubular body and tentacles are full of the green chlorophyll that is characteristic of the plant. Careful examination alone provides the explanation; for it shows that the chlorophyll belongs, not to the animal *Hydra*, but to minute plants that live inside it. There are two creatures here, an animal and a plant, and their association is for mutual benefit. The oxygen set free by the plant and the starch that it makes are used as food by the *Hydra*; and the nitrogen cast off as waste matter by the animal is used by the plant. A more familiar instance of symbiosis is the lichen, an asso-

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ciation between two plants, an alga and a fungus. More striking still, perhaps, is the partnership between the crab *Melia* and the sea-anemone, which it carries about in its claws and which it uses as a weapon and food-getter.

Symbiosis must be distinguished from another kind of association in which one creature lives at the expense of another less intimately, but gives nothing in exchange for the benefit it receives. On the other hand it does no harm. Such associations are called instances of commensalism, and the habit of the sea-anemone *Adamsia palliata* of living on the borrowed shell of the hermit crab *Eupagurus prideauxi* is an example of it.

Such associations help us to understand the parasite, because parasitism is only one more example of the way in which two or more living things may live together. We have only to imagine an instance of commensalism in which one partner not only does not benefit the other, but actually does it harm, and we have almost a definition of true parasitism. Damage—that is the essential feature of the parasite. It harms its associate, and by that harm is distinguished from both the commensal and the symbiont.

That this is still not quite the whole truth about the parasite we shall realise if we consider for a moment that type of the individualist, the carnivore. Consider the man-eating tiger for example, roving abroad, bloodblind, preying upon all flesh. Not a whit less individualistic, though to the human mind less impressive, is the ungulate, the wild antelope, the bison or the giraffe, which preys no less, but whose appetite is for the vegetable world. Both are adventurers, obedient without the capacity for reason, to that primitive philosophy—primitive at least as we human beings see it—which eschews altruism and to which Nature has been faithful from the beginning; and with them stand countless rovers and robbers belonging to every

group of the animal kingdom. In the water these predators range from that marvellous swimmer the cormorant to those aquatic terrors the larvæ of dragonflies which help us by feeding on the young stages of malaria-carrying mosquitoes and of gnats; on the land, from the great cats like the jaguar and the lion to the carnivorous slug *Testacella*, the so-called Gardener's Friend, which is so easily distinguished from all other slugs by the little shell it carries on the end of its tail. Many other predators there are which may be useful to man. Some of them are described in *Insects*, in this series.

A fascinating volume could be written about such rovers and robbers, for all of them show that striking beauty of swift movement and almost incredible efficiency of response and co-ordination of complicated muscular action which is their mark and the imperious condition of their success. But their immediate interest for us is the fact that it is not a far cry from them to some forms of the parasite. The human ironist, taking the no less human "hanger-on" as his sample of the parasite, may remark that such social pests are only less courageous or more sophisticated than the brigand; and we shall not find it any easier to mark the animal parasite sharply off from the predator. The only distinction that we can draw between them is the rule that the parasite is generally smaller and weaker than its prey, while the predator is usually bigger and stronger.

We have thus as complete a definition of the parasite as the present state of our knowledge allows us to make. It is admittedly vague; and the difficulty we find in distinguishing more clearly between the parasite and on the one hand the predator, on the other the commensal, the symbiont, and the saprobiotic creature, is an excellent example of the ever-present and capital difficulty of the biologist. He deals with things that are alive, and whatever lives is in a state

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of constant change. He cannot, therefore, expect to satisfy that human desire, derived we know not whence but certainly a widespread plague, to ticket all things and put them neatly into separate compartments. Nature abhors such rigid categories. She works by slow changes that leave in their train innumerable connecting links between whatever units are distinguishable in the protean web of life. She presents us, for example, with parasites derived from a predatory ancestor; others she shows us descended from the symbiont or the commensal; and as if the connecting links between these and the parasite were not enough to confuse us, she shows us also parasites whose ancestors were either saprophytes or saprozoites. We are forced by the facts, therefore, to be content with the statement that the parasite is an animal or plant which lives either inside or on the surface of the body of another bigger and stronger animal or plant which is called its host, and there does it harm.

CHAPTER II

KINDS OF PARASITES

BOTH plants and animals may be parasites, but the parasitic plants can be only briefly mentioned here. An adequate description of them would need a separate volume, and a very interesting and important volume it would be. For, as Professor Mangham points out in *An Introduction to Botany* in this series, the losses caused to agriculture by such parasitic plants have been colossal and still are a serious menace. Quite naturally, perhaps, the average man is more interested in the organisms that attack his health or pocket or his food supply than in such parasitic plants as the Mistletoe, the Dodder, or the other plant parasites that do little harm to man. He is interested also in the creatures that work on his side, as some parasitic plants do. The fungus *Empusa*, for example, attacks and helps to keep within bounds that dangerous plague, the common house-fly; and there are others.

But among the plants there is, of course, one group of microscopic organisms whose importance to man is incalculable, for they not only help him, but can cause very serious diseases in him and his allies. This group, called the Bacteria, familiarly known as microbes, or germs, and including the rod-shaped bacillus, the globular coccus, the twisted spirillum, and others, may be regarded as a group of lowly organisms which have not developed far beyond the primitive jelly, or we may look upon them as very lowly plants that have developed along a line of their own and have evolved a particular mode of parasitism. Allied to them are the *Spirochaetes*, of which the organism which causes syphilis is an example; we cannot say yet whether the

so-called "filter-passers" and "ultra-microscopic viruses," about which we hear nowadays so much, but which we understand so little, are organisms at all.

All such plant parasites, because of their minute size, their phenomenal powers of increasing their numbers with extraordinary rapidity, their resistance to adverse influences of all kinds, and the ease with which they can be transported in great numbers by the air, by water, or by the bodies of man and of animals, are among the most formidable enemies of other living things. The study of them forms a separate and difficult branch of biology called Bacteriology, and a separate volume would be required for an account of this. We can say no more about them, but must concentrate our attention on the animal parasites.

If we do this we shall find it possible at the outset to divide animal parasites into two groups according to their position either inside their host or upon its surface. Those which, like the threadworm *Enterobius* (*Oxyuris*), so common in children, live inside their host's body, are called *Endoparasites*; those which, like the louse of man or the cattle tick that transmits from cow to cow red-water fever in England and on the Continent and especially in tropical countries, are called *Ectoparasites*.

The fact that some parasites may spend the whole or the greater part of their lives either on or inside a host suggests another kind of grouping. Parasites may be *permanent*, such as the Trypanosome, which has lost entirely the power of living outside the body of a host; or *temporary*, like the leech, which sucks the blood of other animals but also lives a free life in fresh water or in the sea. Permanent parasites are usually more altered by their parasitism than the temporary ones are, and intermediate grades of modification occur which connect these two as they connect all biological categories. The temporary parasite has also been called a *periodical* parasite, a name which draws attention to

the fact that its parasitism is, so to speak, an episode in its career, although it is an experience which regularly recurs and which it must encounter for a certain period. At those periods of its life when it is not parasitic it can live as other free-living animals do.

This parasitic phase may be the fate of the young creature only, as it is of the caterpillars of numerous insects of the group to which the ants and wasps belong. *Cestrus ovis*, the sheep nasal fly, is another instance, its caterpillar stage alone being parasitic in the nasal cavities of sheep, causing serious disease there, the chrysalis and mature insect both living in the world outside. More remarkable, because it occurs in a group which shows very few parasites, is the *Glochidium* larva of the common fresh-water or swan mussel of our ponds and streams, *Anodonta cygnea*. The young of this animal grow up between the lamellæ of the gills of the parent until they have a bivalve shell provided with hooklets on its inner faces, a muscle to open and shut this shell, and threads like the so-called "beard" which attaches the sea mussel to rocks and piers.

These young have no alimentary canal and they cannot live independently. They must trust to chance to send near to them certain fish whose approach stimulates to activity the muscle operating the shell, the two halves of which are then rapidly opened and shut. This violent clapping of the valves drives out the threads of the "beard" and again all depends on the chance that either these or some part of the shell will touch the fish. If this does occur, the two halves of the shell snap shut, the hooklets are buried in the fish's skin or gills or other external soft part and, irritating it, cause a growth of tissues round the glochidium larva, which thus becomes enclosed and may live on the juices of the fish for two to six weeks while the organs of the adult stage are developed. The whole process has been interpreted as a device to ensure that

the offspring of the slow-moving mussel may be disseminated by the active fish over much wider areas than would otherwise be possible, and is contrasted with the other method of achieving the same object by an active free-swimming larva; but it also exposes the species to considerable risk that a high proportion of its young may not survive at all, and in this respect may be compared with the similar risks encountered by the parasites discussed in Chapters VII. and VIII.

The human embryo, living inside its mother's womb, is, strictly speaking, another example of this temporary parasitism of the young phase of the species. That it is a true parasite is undoubted, for it is dependent entirely for food on its mother, and by taking food from her does her considerable damage. The fact that this damage is counted normal and necessary by us, because, like other animals, we obey a deep-seated urge to propagate our species, is apt to make us forget that the damage done amounts to quite as much as that effected by some other parasites; and if anything goes wrong with the growth of the embryo, we know that it quickly may destroy the mother altogether. There could be no better instance, in fact, of a temporary but obligatory parasite than the human embryo.

Other temporary parasites are parasitic when they are sexually mature, the young stages being free-living. Of this there are many instances. The young stage of *Ancylostoma*, the human hookworm, for example, is saprozoic in the soil, and this larva enters man to become sexually mature in his body. Under this heading, too, we must place many creatures which, like the gnats and mosquitoes and the fleas, are ectoparasites and very transient in their parasitism, although their brief attention to man at least may suffice to inoculate into him fatal poisons. We approach here once more to the vague border-line between the parasite—and especially the temporary parasite—and the predator. For obviously all the predators, which, like

the birds and mammals and beetles and other creatures which raid our crops, or even the clothes moths and furniture beetles and booklice and others which attack our household gods, are not far removed from the temporary parasites.

Yet other periodical or temporary parasites are parasitic throughout their lives. Of this a good example is the common cattle tick, *Ixodes ricinus*, which carries red-water fever from beast to beast. From the eggs laid by the adult female of this species a six-legged young stage emerges. This larva has no wings, but lying in the grass it comes into contact sooner or later with a cow and crawls up on to its skin. Piercing the skin with the stylets in its mouth, it sucks blood until it is gorged. It then drops off on to grass, ceasing to be parasitic. A period of free life follows, during which it grows, sheds its skin, and assumes a new one. It is now called a nymph and has eight legs. This nymph attacks another beast and sucks more blood, becoming parasitic thus for another spell. When gorged it drops off once more and moults again. The final stage is the adult tick, and this again becomes parasitic for a longer period. The tick, therefore, is a good example of a temporary or periodical ectoparasite: and the fact that it must be parasitic if it is to complete its life history introduces us to another category.

If the Cattle Tick found no opportunity of sucking blood it would die. It is, therefore, what is called an *obligatory* parasite, and it must be distinguished from such a temporary parasite as, say, the maggot of the blowfly when it enters foul wounds or sores on a human or animal body and develops there. Normally it is not parasitic in such positions, but develops wherever the eggs are laid, in decaying organic matter of almost any kind. The fact that it can be truly parasitic if the eggs are laid upon the sores of living animals makes it a *facultative* parasite: the fact that it can, and in this instance usually does, develop else-

where, distinguishes it from the obligatory parasites which must at some stage be parasitic or die.

These facultative parasites are interesting because a great many of them are saprobiotic in free life. Many roundworms, for example, live in the soil so long as food is abundant there; but when the food supply fails or grows slender, they can enter animals or plants and live in them. The roundworm, *Leptodera appendiculata*, for example, lives normally in damp earth, but it can become parasitic on the slug *Arion empiricorum*, and when it does so it grows larger, loses its mouth, and produces more eggs. These, as we shall see, are normal results of parasitism, but, in this particular instance, before the worm can become sexually mature it must resume its free life. We can therefore say that it is not yet fully established as a parasite. It is a good example of what the great French parasitologist Brumpt has called *inchoate* parasitism, and shows us a species which may, in effect, be actually slowly abandoning free life for parasitism before our eyes. It is probably the adaptation of such creatures to the saprobiotic life that makes it so easy for them to change temporarily to the parasitic way of living, for after all the change is relatively slight. It is in essence a change from life in one kind of dissolved organic matter to a similar mode of life in another. But the importance of such a possible change is obvious. If such a saprobiotic creature loses the power it once had of going back to the saprobiotic mode of life in dead organic matter it becomes an obligatory parasite.

If we like to multiply distinctions further we can establish a category of *accidental* (or incidental) parasites to include all those creatures which live usually a free life but are only occasionally found living parasitically in or on another animal's body. Some of the *Myriapoda* (the group which includes the Centipedes and Millipedes), for example, can live for several days in the human body.

Some other parasites normally occur in only one species of host, but may now and then live in other species. These also have been called *accidental parasites*. The worm *Echinorhynchus gigas*, for example, is normally found in the pig, but may occur in man occasionally; the common liver flukes *Fasciola hepatica* and *Dicrocoelium lanceolatum* found in sheep and other mammals, may occur in man; while the broad tapeworm of man, *Dibothriocephalus latus*, characteristically parasitic in him, may be also found in the dog, the cat, and the fox.

Two other categories of parasites remain to be considered. The first of these have been called *hyperparasites* or auxiliary parasites, and they illustrate the much-quoted rhyme :

“The little fleas have lesser fleas
Upon their backs to bite 'em,
And the lesser fleas have other fleas,
And so—ad infinitum.”

“Ad infinitum” expresses, we must confess, poetic licence rather than the truth; but it is true enough that parasites are themselves attacked by other parasites, and instances are known of yet a third parasite of the parasite of a parasite.

This fact has been utilised by those whose business it is to rid our crops of the animal scourges which attack them, but, although some of the parasites that cause disease in man may also suffer from parasites, it has not yet been possible to try to control these latter in the same way. As Professor Balfour Browne points out, moreover, in *Insects* in this series, we must, if we try to control any agricultural pest by encouraging the multiplication of the parasites that attack it, take care that the parasite itself does not become a worse scourge than the original pest. The practice of such a method is, furthermore, always a difficult matter. For to be successful with it we must be sure that we are able to

rear these hyperparasites in sufficient numbers, that they are not likely to lay their eggs on other hosts which may be equally favourable to them and so may absorb all the parasites and let the creature we are hoping to exterminate go free, that there is a host on which our helper can live at those periods when the enemy is absent, that our helper has greater fecundity than that of the enemy, that its cycle of development is quicker, that it is less sensitive to climatic influences than its host, and that it is free from parasites itself.

These conditions are not easily fulfilled, and this form of biological attack is therefore far less readily launched than might be expected. Nevertheless, it is being actively exploited to some purpose. There is a station at Farnham Royal, Bucks, from which such insect helpers of man are exported to our colonies, where they can be of great value; and other countries have similar stations.

One other use of the parasite in a similar way is worth noting. It has been found that people suffering from the disease called General Paralysis of the Insane sometimes benefit if the parasite that causes malaria is introduced into their blood. How this beneficial influence is exerted cannot be explained here, but it is another instance of the fact that one parasite may help to neutralise the harmful effects of another.

Finally, there is the category of the so-called *pseudo-parasites*, against which the parasitologist must always be on his guard. The doctor especially needs to be familiar with these, for again and again he encounters, in the urine and fæces and other excreta and in the juices of his patients, animals and plants which may or may not be agents of disease. He has to decide whether these are real parasites of his patient, or whether they have been merely accidentally introduced into the body or have got into the material he is examining after it left the body. In the alimentary tract, for example, numbers of protozoa and eggs of

worms and even the caterpillars and chrysalids and eggs of insects may be found which have been introduced with the food and drink. They are merely passengers there and have no effect on the patient. Introduced by the mouth, they are either destroyed by the digestive juices or resist them and pass out again and resume their normal development in the world outside. Some of them may have got into the fæces and urine after these have left the body. Adult insects and their grubs may, for example, be attracted by the odour of these and may either feed upon them or deposit their eggs in them. The detritus of vegetable matter, the various forms assumed by partially digested food, animal and vegetable matter that may have fallen into the fæces or urine from the air itself, or shreds and threads of garments or other fabrics, may all lead to errors of diagnosis, especially because some of them are, to the inexperienced observer, extremely like the true parasites of man. This kind of difficulty is enormously increased when an animal is being examined, because the chances of contamination of its food, drink, or excreta are very much greater.

CHAPTER III

DISTRIBUTION OF PARASITES

A. ZOOLOGICAL

BECAUSE the parasite is smaller and weaker than its host and because, as we shall learn in the next chapter, the adoption of the parasitic mode of life involves profound changes in the parasite's structure and physiological processes, we should not expect to find that many of the backboneed animals have become parasites. For they are, speaking generally, the largest of animals. Their bulk, their relatively heavy and resistant skeletons, and the complex structure of their bodies, must all have worked against success in parasitic life. They were, moreover, the last members of the animal series to appear and have therefore had less time in which to adapt themselves to such a mode of life. More potent reason still, they are more efficiently equipped for the battle of life than any other kind of animal, and have actually been more successful, unless we count the ubiquitous insects as their equals in this respect. This very success, proved as it is on the land, in the air and under the water, may have determined the fact that they have so little explored the possibilities of parasitism.

There are, however, one or two interesting vertebrate parasites. With the exception of the few species of bloodsucking bats, of which *Desmodus rufus* is an example—the so-called "vampire" not sucking blood at all—vertebrate parasites belong, it is worth noting, to the lowest section of that series, the fishes, and two of them to the group called the *Cyclostomes* or round-mouthed fishes, which stands at the very root of the

vertebrate stem. These two are *Myxine*, the hagfish, and *Petromyzon*, the lamprey. The hagfish is the more formidable, for it not only, like the lamprey, inflicts grave wounds on other fish and aquatic creatures by rasping off their skin and flesh with the horny teeth inside its suctorial jawless mouth and on its pistonlike tongue, but by means of these teeth and its tongue it can also bore deeply into the muscles of its host, burying its head and the fore-part of its body in them. In order that it may breathe while in this position, the inlet of the water of respiration is not by the mouth, but through two small pipes which lead to the gullet from two small holes far back on each side of its eel-like body, and this water, after passing over the tufts of bloodvessels in the gill pouches on either side, finds its way out again by tubes which lead to the same pair of holes. The fish's method of breathing by the intake of water through the mouth and its passage over gills and out again by several separate gill-slits, has thus been modified by the parasitic habit of this creature.

If, however, the vertebrates show us very few real parasites, the very reasons given above for their failure to explore this mode of life—namely, their large size and the complexity of their organisation and the high degree to which its control and co-ordination have been brought—make them very successful predators and robbers. They all are, moreover, in a sense, parasitic on the vegetable world, for, like every other animal, they depend for their existence, at one or more removes, upon plant life. But their main interest to the parasitologist is that they provide the food and dwellings of parasites rather than examples of parasitism itself. They are the hosts, *par excellence*, and very few of them have escaped the attention of one or more uninvited guests.

Three other great groups, or phyla, of the animal kingdom show us, like the vertebrata, very few parasites. These are the *Cœlenterata*, a group which

includes the sea anemones and corals and their like, and among which we find many sedentary animals but few real parasites; the *Echinodermata*, comprising the starfishes, sea-urchins, sea-cucumbers, and similar species; and thirdly, the *Mollusca*, often miscalled the shellfish, in which group occur many creatures which, like the piddock (*Pholas*) and the shipworm (*Teredo*), bore into rocks or ships and piers and other marine works of man, but which cannot for this reason be called parasites. Other shellfish approach near to parasitism through the habit of commensalism, and some of them, like the young stage of the freshwater mussel already mentioned, are really parasitic. Others are usually parasitic upon the bodies of *Echinodermata*. They may be either ectoparasitic like the comparatively unaltered *Thyca*, which lives on the bodies of members of the starfish group, or they may be endoparasitic, and are then much more altered by their parasitic life.

Three other big groups of the animal kingdom remain, and to these most of the parasites belong. These groups are the *Protozoa*, the earliest group to appear in evolutionary history, the rather loose collection of creatures which some writers call the *Vermes*, or worms, and the most highly organised of the backboneless animals, the *Arthropoda*, or creatures with jointed limbs. Let us look at these briefly in turn, beginning with the worms.

The animals that used to be grouped under the general term *Vermes*, or worms, are now subdivided into several groups. The types of them most familiar perhaps are the earthworm, the lugworm of our shores, the leech, and the tapeworm. The parasitologist is not concerned with the groups to which the lugworm and the earthworm belong. The leeches are external bloodsucking parasites of man and other animals. They are able to make within their bodies a fluid which they squirt into their victim's blood, and

which prevents the clotting of its blood, so that their meal is assured; and the part they play in the transmission of disease will be referred to below. Most of the other worm parasites belong either to groups known as the *Nematoda* or Roundworms or to the *Platyhelminia* or Flatworms, the English names of which refer to the characteristic shape of the body in each group; and all of these have progressed in parasitism further than other parasites have.

Among the flatworms, however, we find a section called the *Turbellaria*, or Eddyworms, which are not parasitic, though many of them are carnivorous and must be counted among the most terrible of the smaller freshwater and marine predators. They interest the zoologist because it is probably from creatures like them that the other flatworms, the flukes and the tapeworms, have been derived. Let us be clear about this. It is not suggested that a modern tapeworm or fluke arose from a modern free-living eddyworm, or even that such a direct transition as this occurred in the past. The suggestion is rather that all the flukes and tapeworms probably arose from the ancestors of the modern eddyworms, a hypothesis which can be expressed, as can all evolutionary descent, better by comparison with a system of rivers than by the familiar and often misleading form of the branching genealogical tree. For rivers are often difficult to trace to their sources from other streams, or from the subterranean waters. They may pass underground and appear to arise anew; and we have to dig long and patiently to find their origin. So with animal groups. We are still digging, for example, for the source of the vertebrate river, for the origin of the sluggish molluscan canal and for the exact point in the ancient marsh of early organisms from which began the twin streams that we call animal and plant.

Somewhere near this point began, we must believe, a fascinating series of creatures which we call the

Protozoa, most of which are microscopic in size and very difficult to study. They may be parasitic on the surface of animals, but the majority of the harmful ones are endoparasitic. Malaria, sleeping sickness (but not "sleepy sickness," which is caused by one of the bacteria), the oriental diseases kala-azar and tropical ulcer, amœbic dysentery, and red-water fever of cattle, are only some of the serious diseases due to them. It can be truthfully said that the comparatively new branch of zoology called Protozoology presents the most difficult and intricate and perhaps for that reason the most fascinating of all problems for the modern biologist. We shall see in subsequent chapters how closely it is bound up with the study of the parasitic members of the third great phylum of animals that includes great numbers of parasites, the *Arthropoda*.

This enormous group, including as it does the crustacea, to which section such creatures as the crab, the lobster and such parasites as the whale-lice belong, the centipedes and millipedes, the spiders and scorpions, and the great series of insects, is of great importance to the parasitologist. To the economic parasitologist, he who studies parasites as they affect man himself and all his creatures, this group will seem of great importance because members of it transmit other parasites from host to host and spread them thus about the earth; but he has to deal also with those other members of it who are active parasites themselves, either on the surface of or inside both man and his domesticated animals, or as enemies of the farmer.

B. DISTRIBUTION IN THE HOST

No animal is free from parasites, and no tissue of the body escapes them, although some animals, and some tissues and organs, are more liable to attack. The vertebrates, for example, suffer more than the

backboneless creatures do, and certain organs, such as the skin, and notably the alimentary tract and appendages of it like the liver, being more accessible to potential parasites living in the outside world, are often the first organs to be attacked. Once established in such situations, the parasite may not spread to other organs; but many parasites that began in the alimentary tract especially, have extended their habitat, and either journey for periods through the body tissues, returning "home," as it were, to the intestine, or leave it entirely to take up their abode in the deeper tissues.

That animals are not the only hosts of parasites we have already learnt. Plants also are attacked, and the serious damage done to wheat and other cereals, to beet and various bulbs, by the roundworms that we call "eelworms" of various kinds, brings home to us the fact that many organisms living in the soil can leave it to damage our crops. They may also harm our animals and even ourselves.

The *geographical distribution* of parasites corresponds, of course, to that of the hosts in which the parasites live. We have space to do no more here than to draw attention to the fact that all parasites are more abundant, as is all plant and animal life in general, in the tropics. We shall learn also, in a later chapter, that many parasites depend absolutely for the completion of their life histories upon a second host which transmits them from the vertebrate in which they live to another individual of the same species; and in this second host, which is usually a bloodsucking insect or other invertebrate, part of their life cycle must be passed. This means that the distribution of such parasites will correspond exactly to that of the second host without which they cannot continue to live; and this fact may have great practical importance. The trypanosome, for example, which causes sleeping sickness in man in Africa, depends entirely on the tsetse fly, in which alone it can pass a part of its life history. We

can be sure, therefore, that where that tsetse fly does not exist, that form of sleeping sickness will not trouble us either. The same is true of malaria, of the red-water fever of cattle transmitted by ticks, of some of the diseases caused by tapeworms and flukes and of other maladies.

The distribution of parasites in *time* is largely a matter of conjecture. Their particular mode of life means that the hard parts which are most often preserved as fossils are lost before the parasitic life can be successful. What parasites, for example, infested the great intestines and other organs of the giant reptiles that once lived on the earth and in the air and water, we do not know. It is conceivable that such parasites played some part in the overthrow of this enormous race. The bacteria certainly must have been myriad Davids to threaten incessantly these Goliaths. We cannot ascribe to them all the power which H. G. Wells allows them when he makes them the only earthly power that could kill his men from Mars, but, in common with other parasites, they must have been a factor in the downfall of every race that is now extinct.

CHAPTER IV

EFFECTS OF PARASITES UPON THEIR HOSTS

SEVERAL factors determine the nature and extent of the damage done by a parasite. Its *position* in the host's body may influence what we call its pathogenicity or capacity for doing harm. This position will not necessarily depend upon the way the parasite enters the host. It may enter passively, without effort of its own, being carried to the host by the air, or in the food or drink, by the sexual act, or by the bites of bloodsucking ectoparasites, or even by the blood of the host which takes it to the egg or embryo while this is still in the parent, so that the young are born with the parasite already in them. Or it may enter by an active effort of its own, as when the young of the miner's hookworm penetrate the skin of man, or the miracidium larva of the liver fluke bores its way into the snail *Limnæa truncatula* (see Chapter VIII.).

But the endoparasite, at any rate, rarely remains near the point at which it entered. Usually it migrates or is carried by the blood to other parts, and its position in those parts may help to determine the damage it can do. It may reach a vital organ and settle down in it, as when the egg of the tapeworm *Tænia cœnurus* of the dog is eaten by a sheep and grows into a bladderworm which settles in the brain or spinal cord of a sheep and causes the disease called staggers or gid, the symptoms of which are due chiefly to the pressure exerted by the bladderworm on the brain. This pressure causes disturbances of co-ordination of movement such as a staggering gait, a frenzied careering about a field in circles towards that side of

the brain on which the bladderworm lies, or the turning of somersaults. Particular symptoms are also caused according to the position of the parasite in a particular part of any organ it may inhabit. If the bladderworm that causes gid settles in the front end of the brain it will not do so much harm as if it settles farther back in the part of the brain that contains vital centres of nervous activity such as those which control the heart's action or the breathing. If it settles in the spinal cord alone, it will cause paralyses and spasms of those parts only which are controlled by that section of the spinal cord which it inhabits.

The similar bladderworm of the armed tapeworm of man may develop in him as well as in the pig, in which it is normally found, and, if it does so, may reach the eye and cause inflammations and opacity of the lens there, or may settle in the brain and cause headaches and cerebral anæmia due to its pressure upon the arteries that supply the brain with blood, or distension of the brain with fluid (hydrocephaly). By the irritation of the nervous tissue it may, like the parasite of gid, cause epileptiform attacks, and it may also settle in the heart muscle, when fainting fits and attacks of shortness of breath result. People who, by eating pork containing these bladderworms, acquire this tapeworm should be very careful, therefore, that they do not in any way swallow the eggs of such worms with their food or drink and so infect themselves with the bladderworms as well. Fortunately in this country the habit of cooking pork thoroughly and the very efficient inspection of meat carried out everywhere reduce very greatly our liability to this form of disease.

Such bladderworms as these are good examples of the way in which the position of a parasite may determine the damage done, because although the ingestion of tapeworm eggs means usually that numbers of these bladderworms may be disseminated throughout the

body, only those which settle in vital organs cause disease. All those which settle in the muscles, for example, are normally enclosed, by a reaction of the connective tissue that lies between the muscle fibres, in a protective case of this tissue and remain there comparatively harmless.

Some internal parasites, however, habitually attack certain tissues only. The roundworms generally live in the small intestine near to the stomach, into which they may also penetrate. One of them, *Strongylus gigas*, attacks the kidney. Another, *Syngamus trachealis*, the worm that causes gapes in poultry, settles in the windpipe, while the worms that cause husk in cattle and sheep also live in the lungs and air tubes. *Trichinella spiralis*, another roundworm, occurs in the voluntary muscles, and is found in greater numbers in the muscles of the midriff, those between the ribs and those of the throat and neck.

Some endoparasites attack the blood especially, either swallowing it, as do some roundworms, the fluke and the leeches and other bloodsucking ectoparasites, after they have broken a way into the blood-vessels either with their teeth or with piercing mouth-parts, or, like the roundworms of the genus *Filaria* and the *Trypanosomes*, living in the blood as in a bath and absorbing it as food. Others, such as the parasites that cause malaria, consume the substance of the cells of the blood.

Endoparasites may also feed upon protoplasm itself. The protozoan parasites that cause a form of white diarrhoea in poultry and cattle consume, for example, the cells that line the intestine; others, like *Entamoeba histolytica*, the cause of amoebic dysentery in man, make for themselves a ferment which dissolves the lining of the intestine into a kind of soup, in a bath of which the parasite lives and which it absorbs as food. This habit of some parasites of feeding on an exudate provoked by their own damage is an interesting one. It is

paralleled by the human idea of scarring a gum tree to get the resin that exudes from the wound. The mite, *Psoroptes*, which causes the disease of sheep called scab, feeds thus upon the blood serum exuding from the bites it makes; and the grub of the warble fly, which can be such a serious pest of English cattle, causes, beneath the skin of the back of the beast, offensive sores full of matter in which the maggots find their nutriment.

One is almost tempted, in the light of such instances as these, to say that a parasite "selects" its habitation and seems to work with a purpose, but we are not justified in introducing such human conceptions as purpose and choice into interpretations of animal behaviour. All that we know about the behaviour of other animals teaches us that such apparent selections may be merely the result of chemical attractions exerted by the tissues upon the parasite.

The movements of parasites must in themselves be considered as possible causes of injury. The rheumatoid pains and fever due to the presence in man of the roundworm *Trichinella spiralis*, taken in by eating uncooked pork infected with it, are caused by the mass migration of numbers of the young of these worms from the intestine to the muscles. Once they have settled down in the muscles the symptoms cease and the parasites not only do no further harm, but usually are encased, as other foreign bodies often are, by a wall of connective tissue formed by the host, in which chalky matter may be deposited later and in which the parasite eventually dies. The eggs of the fluke *Schistosoma* (*Bilharzia*), which causes a serious disease of the urinary organs in man in the tropics, are provided with spines, the irritation of which produces inflammation of the bladder and of the end of the digestive tract characteristic of this malady, for they work their way out of the tissues in which they are laid into these natural outlets to the outer world where the young

stages of the parasite must seek the snail, inside which they must live for a while.

If for any reason the complicated journeys often undertaken by parasites are not completed, as when, for example, the young of the roundworm *Ascaris* are carried by the blood to the liver and remain there or do not pass beyond the lung, they may cause irritation or disease wherever they settle.

Most of the instances so far cited might be included under the heading of mechanical damage or irritation. With them we should include the bites of fleas, lice, mosquitoes, bed bugs, ticks, leeches, and such other temporary ectoparasites as the bloodsucking bats.

Many parasites, however, obtain their food without doing much mechanical damage to their hosts. Such are creatures like the parasitic crustacea mentioned in Chapter V., the rootlike processes of whose bodies may branch and ramify throughout their hosts without doing to them vital harm. Indeed, they may often avoid, as do the "roots" of *Sacculina*, for example, vital organs like the heart and gills of the crab it lives on, although they penetrate into every other part. The effect of this particular parasite is extremely remarkable, for the female crabs are little altered, but the males acquire the secondary sexual characters of the female, so that they resemble them externally, undergoing what is called "parasitic castration."

Among such general effects we must also include the harm done by the tapeworms, whose suckers and hooklets do little harm in themselves. The damage done by these parasites is due to the fact that they can steal the host's food to such an extent that wasting and ill-health result. This effect may be more serious if the host is young or very old, a factor which is important whatever the method of damage employed by the parasite. The importance of the age of the host is obvious when we learn that not the least damage a parasite may do is to lower the general health of its host to

such an extent that it is predisposed to other diseases. Certain poisonous substances, or toxins, may also be produced by some parasites. The trypanosomes, for example, may set free such poisons into the blood; and although much doubt has recently been cast on statements about the power of these poisons, the existence of many of which has been denied, they certainly must be reckoned among the ways in which a parasite may damage its host. Against them the host produces anti-toxins, which may confer upon it a passive immunity.

The secretions made by parasites are an interesting study, but lack of space forbids our entering into it here. It is worth while, however, to record the fact that some of the parasitic worms, and probably other intestinal parasites as well, secrete a substance which prevents the digestive juices of their hosts from digesting them. Thus is answered the question asked by many investigators: Why is not a parasitic worm digested like any other flesh in the gut?

The number of parasites present in any host is obviously another important factor in determining the amount of damage they can do. If a parasite multiplies outside its host, as the liver fluke does, for example, its chances of doing harm are less than if, like the parasite causing malaria, it can multiply within the host's body. Large numbers of a small parasite may cause more harm than a few large ones. Something will depend upon the relative virulence of parasites, and upon the relative virulence of different strains or stocks of them; but the harm done by such microscopic creatures as the trypanosome or the parasite of malaria, which have phenomenal powers of rapid multiplication, generally exceeds that done by such larger endoparasites as the tapeworm. The latter can also reproduce large numbers of offspring; in fact, we shall learn below that it is a feature of parasites in general to be able to do so, but the tapeworms do it more slowly. It is the rapidity of multiplication that

makes creatures like the malaria parasite so harmful. Their capacity for rapid reproduction is only excelled by that of those extraordinarily prolific parasitic plants, the bacteria, and by both it is effected by such non-sexual methods as division of the parent into two or many parts simultaneously produced, this being the phase which usually does the damage.

Growth of the parasite, combined with its existence in large numbers, may be serious in its effects. Thus *Fasciola hepatica* can block up the bile ducts of the liver, the roundworms of the genera *Filaria* and *Strongylus* may block up blood canals and so cause clotting of the blood and swelling and weakening of the walls of the bloodvessels, with the consequent danger that they may burst. Back pressure, too, upon the organs from which the bloodvessels are bringing blood may cause consequent disease in them. Another interesting instance of a disease caused by this obstruction of vital canals by parasites is the Isle of Wight bee disease, due to the blocking of the breathing tubes of the bees by the mite *Acarapis woodii* that is parasitic within them.

Finally, we must not forget that temporary blood-sucking parasites of all kinds damage other animals by the mere fact that they may suck up with each feed blood parasites which they transmit to other individuals. The mosquitoes which thus "carry" malaria from man to man, the tsetse flies which transmit the trypanosomes that cause sleeping sickness, the ticks which pass red-water fever from cow to cow, the sand fly that is being nowadays convicted of transmitting the disease called kala-azar that attacks the Indian and some other tropical peoples—all these are the enemies of vertebrate animals in this respect. The leeches also distribute trypanosomes and other blood parasites among the fishes and other aquatic animals both in fresh water and in the sea. Nor should we forget such creatures as the dog-louse and the dog-flea, which trans-

mit the tapeworm *Dipylidium caninum* of the dog, and may so communicate the worm to children, because the dog may chew up the lice and fleas and then lick the child, and so infect it with the bladder-worm stages that grow up in the child into the tapeworm. The snails which transmit certain stages of the fluke *Schistosoma*, the "water-flea" *Cyclops* and the fish which together transmit the broad tapeworm of man in the Baltic region, and many others of the intermediate hosts described in Chapter VIII., must also be included here.

CHAPTER V

EFFECTS OF PARASITISM UPON THE PARASITE

IN an earlier chapter the statement was made that the parasitic life causes characteristic changes in the parasite's structure. It also leads to physiological changes and to the acquisition of new characters. This will be clearer if we consider first the relatively simple instance of an ectoparasite.

On the wool and skin of sheep there is often found in this and other countries a creature called the sheep ked (*Melophagus ovinus*), often miscalled a tick and mistaken for one. Close examination shows, however, that the sheep ked has but six legs, while the tick has eight, and that the body of the ked is divided into head and thorax and abdomen, a feature which, taken with the number of legs, proves it to be an insect, and, not like the tick, a member of the *Arachnida*, the group to which the spiders and scorpions belong.

Yet how different from, say, a dragon-fly or a moth, is this dark brown, loathsome, bloodsucking parasite, with its leathery hairy integument, its long, strong, active legs each ending in strong curved claws. And it has no wings at all. The only traces of them are two disclike vestiges on the skin of its thorax. Remarkable does it seem that this crawling pest can be blood brother to such a beautiful and very active creature as, say, the hover fly, that hangs so marvelously in the sunlit air of our gardens, and, warned by its wonderful eyes and nervous system, darts away at our approach, or the delicate midge, whose activity and high efficiency none of us can deny, or even the

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house fly or blue-bottle, that we rightly destroy if we can.

Yet true it is. The sheep ked is a dipterous or two-winged fly, that has been so altered by its parasitic life that it is scarcely recognisable. Instead of the grill-like proboscis by which the house fly gathers up the food which it has liquefied, or the chewing jaws of a beetle, or the coiled sucking tube of a moth or butterfly, its mouthparts are pointed for piercing the skin of its host whose blood it sucks. Its leathery skin is a protective armour. The hairs on its body are all directed backwards so that it can move with the strong clawed legs through the forest of hair in which it lives. Claws help it to cling there when the host, irritated by its bites, seeks to dislodge it; and wings it has lost because it no longer needs them. All its life is parasitic on the sheep. Food is plentiful and need not be sought by active flight. Even the reproductive process is altered to suit the mode of life. For the female ked, when her eggs are impregnated by the male, does not lay them as other insects do. She keeps them in her body till the caterpillar stage is formed, and to this she gives birth. Almost as soon as it is born this caterpillar becomes a hard, dark brownish-red chrysalis or pupa, which either remains in the wool or falls to the ground. Here it is capable of living for six weeks, but usually within about twenty-four days the young ked emerges from it and regains the sheep to begin its life cycle again. Since the female can lay a caterpillar every nine days, the rate of increase is rapid.

Such a parasite illustrates well the general principle that parasitism leads to a simplification of structure in the parasite. This principle is often called "degeneration of the parasite," a phrase which is misleading, because it suggests the human conception of decay, or descent from a "higher" condition to a "lower" one, for which there is no place in

biology. We must try all the time to see things from the parasite's point of view, and if we do this we shall realise that what happens to the parasite is simply what happens to every other living thing when it changes its mode of life. It adapts itself to the new conditions it meets with. No laws of biology are broken, no new ones are brought into being. If the sheep ked loses its wings, or the hagfish its eyes, if tapeworms lose their alimentary canal or liver flukes the cilia that belonged to their ancestors, that need not be degeneration; for degeneration implies loss of efficiency, and no one can accuse these parasites of that. All that happens is a simplification of structure, a simplification that is a stern necessity if the parasite is to succeed in its new mode of life. As the great parasitologist Leuckart said: "Je sesshafter ein Parasit, desto primitiver der Bau"—the more settled a parasite, the more primitive its structure.

The same principle can be illustrated by a thousand examples. All parasites tend to lose locomotor organs, for example. They are no longer needed, and Nature dispenses with them. The process may take a very long time to accomplish; and we find, therefore, various degrees of it in various parasites. The sheep ked and the louse have lost their wings entirely; but both sexes of that close relation of the sheep ked, the horse ked, or New Forest fly, *Hippobosca equina*, retain their wings, although they do not use them as much as they might do, preferring to run between the hairs of the host. It will be interesting for some future biologist to find out whether, generations hence, this horse ked arrives at the wingless state of its near relative, the sheep ked.

More striking examples of this loss of locomotor organs can be found, as would be expected, among the endoparasites, because the entry into the interior of another animal must obviously cause a more profound modification of structure than the mere settle-

ment on its external surface. The power of movement, moreover, is not so important to the endoparasite as it is to the ectoparasite and the free-liver, and the primary stimuli that cause the evolution of the power to move—namely, the need to seek food, to chase and secure it by force, the need to seek a mate and copulate with her, and also the need for self-defence against other animals, or escape from them or from other inimical influences, operate less powerfully upon the endoparasite, because inimical influences inside another animal are less abundant, and hunger and sex can be satisfied with relatively little change of position.

Recent work has, however, shown that even the endoparasite moves about in the body of its host much more extensively than was formerly thought. Some of the parasitic roundworms, especially, can carry out remarkable migrations through the tissues (see Chapter VI.). Even the tapeworm lying in the intestine may execute considerable movements, although there may seem to be little reason why it should do so, because it lives in a bath of food which it takes in through its soft skin. To effect a fertilisation of the eggs in each of the flattened segments of which it is composed, all that is necessary is that the genital pore at the side of each of these should be brought into contact with the genital pore of a neighbouring one. This is done by wriggling and contractions of the segments themselves. These segments possess, once they are ripe and ready to be discharged from the body, considerable power of movement by similar contractions, especially if the temperature be suitable. One of the characteristic differences, in fact, between the two chief tapeworms of man, *Tenia solium* and *Tenia saginata*, is the sluggishness of the segments of the former, which move comparatively little, and the activity of those of the latter, which may be entirely beyond the host's control, wriggling their way out of his alimentary canal into his bed or underclothing

before they ultimately succumb to the death and disintegration by which the ripe eggs in them are normally set free.

The tapeworm, however, is not a good instance of the loss of locomotor organs due to parasitism, because its ancestors had neither limbs nor wings. Better examples are furnished by the remarkable series of parasitic *Copepoda*, a group of small aquatic crustacea allied to the lobster, the shrimp, and the woodlouse. Among these there is that type of the active, swift, and efficient predator, the creature called *Cyclops*, common in freshwater ponds, often erroneously called the water-flea and conspicuous as a rule by the presence beside its long tail of a pair of bags of brightly-coloured eggs. The activity, and lightning response to stimuli, and co-ordination of movements shown by this creature are remarkable. It might fairly be described as a small epitome of the qualities required for success in the struggle for existence under the water.

Related to it, however, is the family *Caligida*, similar small creatures which have adopted a parasitic life upon the skin of fishes, whose blood they suck. Since they are ectoparasites, we shall not expect to find them very much modified, and this is so. They have kept, at least, the power of swimming freely. Another family, the *Lernæida*, have, however, been more modified. These are ectoparasites also, the young ones living usually on the gills of fishes of the plaice family, the female alone of the adult stage upon the gills of fishes of the group to which the cod belongs, into which she burrows, holding on by rootlike processes of her head; but her swimming feet have now become mere vestiges. The *Chondracanthida* and *Lernæopodida* show similar modification, but the male is swept into the change, becoming much smaller than the female and also permanently parasitic upon her. Most modified of all are species like *Rhizorhina*, parasitic upon the group of seaworms to which the lug-

worm belongs, and on certain of its own relatives (Crustacea). The female of this species has no limbs at all, and is attached to her host by a tube, which ramifies in its body like a system of roots and carries food to her, whilst a number of males, also without limbs, are attached to her near to her genital opening.

Among the Crustacea, also, is the group of parasitic *Rhizocephala*, which live upon crabs. All of them have lost their limbs, and all trace of that segmentation of the body which is characteristic of all arthropods, and of the complicated muscular and nervous apparatus associated with it, has gone. The alimentary canal has also disappeared. *Sacculina*, for example, already referred to, is little more than a simple flattened sac attached to the abdomen of the short-tailed crab, on which it lives, and in it there is little more than the genital organs.

Remarkable also is the parasitic shellfish *Enterorenos osargreni* found in the intestine of sea-cucumbers. To it remains scarcely any structure by which it can be recognised as a shellfish. To determine the relationships of such profoundly altered creatures we have to study the young that come from their eggs. The egg of *Enterorenos* gives rise to a larva of the kind known as a *Veliger*, which brands its parent as a shellfish. The *Nauplius* larva of *Rhizorhina* and of other parasitic crustacea proves that they could not belong to any other group of animals.

CHAPTER VI

EFFECTS OF PARASITISM UPON THE PARASITE (Continued)

THOUGH the parasite may lose its power of movement, it may acquire new features by way of compensation, and of these the tapeworm shows us one example. The body of this remarkable creature is a chain, often many feet in length, of flattened pieces budded off from a minute head shaped like a club. It has entered the alimentary canal of, say, a dog, which is full of a thick soup of half-digested food, in which the tapeworm must live; and this soup is being more or less constantly compressed and mixed and urged onward towards the vent by the rhythmical contractions of this alimentary tube. The tapeworm has no locomotor organs. How is it to hold its own in this tubular bath; how prevent itself from being swept on to the vent and out into the world where it would infallibly die?

It solves this problem in a way that to us human beings seems obvious. It anchors itself to the wall of the intestine by developing on its head four minute suckers. The oval ones of the beef tapeworm of man are about one-thirtieth of an inch long, and there are four of them at intervals round the head, which is not more than one-twelfth of an inch in diameter. They serve to hold in place a worm that may be a quarter of an inch in breadth and over thirty feet long. The other tapeworm frequently found in man, *Tania solium*, the pork tapeworm, is usually smaller, but it has, in addition to its four suckers, a circlet of from twenty-five to fifty minute horny hooklets which help

the suckers to keep the worm in its place. Such suckers and hooklets are often possessed by parasites of all kinds.

Devices for attachment are, as we should expect, best developed in the ectoparasites, because these, being swept by the water or air in which their host lives, or exposed to its attempts to rid itself of them, need a firmer attachment. And Nature is entirely ruthless. She frowns on half-measures, and, having got rid of locomotor organs thoroughly, works towards the development of equally efficient anchors. Those individuals which fail to develop these are not successful and cannot propagate their kind, so that progressive efficiency in whatever type of sucker or hooklet has been evolved must follow. The same law holds whenever any other method of attachment is developed. The whipworm, *Trichuris* (*Trichocephalus*), for example, and all its near relatives, have not developed suckers or hooklets, but the front third or so of their bodies has become elongated and threadlike and is buried in the tissues of the host. The long protoplasmic process called an epimerite at the anterior end of many gregarine protozoa is another example of this method of attachment.

Just as locomotor organs may be lost by parasites because they are no longer useful, so the alimentary canal may be simplified or disappear altogether; and in this respect again we find degrees of simplification.

If a free-living animal accustomed to masticating solid food takes to parasitic life, the first change may take place in its mouth. Teeth that were necessary for killing and chewing up other animals are no longer needed for either purpose, although the food may still have to be digested, so that the rest of the alimentary canal is little affected. The modification of the mouth of the ectoparasitic insects is a good example of this. Typically an insect's mouth is provided with biting mandibles like those of the cockroach, suitable for

chewing small pieces of food that have been bitten off; but transient bloodsucking diptera, such as the mosquito, the horse fly, or the tsetse fly, all have, instead of such biting mandibles, piercing stylets with which the insect can bore through the skin of its host and reach its blood. The same is true of the lice, the fleas, and the bugs. Among *Arachnida* the ticks show a similar modification. Furthermore, the pharynx of such insects develops into a sucking pump, by means of which either blood or the juices of plants, which they also may suck, are brought up into the stomach.

The roundworms also show alterations in their mouths for a similar purpose. The mouth of *Ancylostoma duodenale*, the miner's hookworm, is shaped rather like a bell, and is provided with horny teeth with which it takes hold of the lining of the intestine. Through the wound thus made the worm sucks the blood of its host. The bloodsucking roundworms that can be such serious pests of sheep and other domesticated animals have a similar apparatus. Some of the eelworms, which cause such diseases of plants as "Earcockles" of wheat and "Tulip-root" of oats, have a spine which they work backwards and forwards, and with which they bore into the host plant. The leeches have numerous small teeth with which they make characteristic often tri-radiate wounds. Interesting also is the difference between the typical teeth of the bats, which are adapted for crushing either insects or fruit, and those of species which, like *Desmodus rufus*, suck the blood of man and animals. These repulsive creatures have developed razor-like incisors and canine teeth at the front of the mouth. With these they make horizontal cuts through which they suck blood; and the grinding teeth at the back of the mouth, being useless to an animal that feeds upon blood, are small and unimportant.

Most of the species just mentioned retain in varying degrees the rest of the alimentary canal. They

are parasites, but even when they live inside other animals they eat solid food, whether it be blood or tissues, and digest it. The common liver fluke of the sheep is similar to them in this respect. It lives in the bile ducts of the liver and feeds there on bile and also on blood which it obtains by breaking a way into the bloodvessels. Some blood-sucking species, such as the leeches, have developed a very capacious crop, provided with lateral pouches, in which they can store up enough blood to last them for more than a year. Such species usually suck blood only occasionally and this storage crop enables them to live between their periodical meals.

Very different from them is the tapeworm, which has no alimentary canal at all. We must suppose that its ancestors originally had one; but life for long periods in a bath of rich food in the intestine, food which it can absorb already half-digested through its soft skin, has rendered an alimentary canal unnecessary.

The ability of the tapeworm to absorb and utilise, without the help of an alimentary canal, the half-digested food of its host is very remarkable. It is one of the new characters acquired by these creatures as a result of parasitic life, and it directs attention to the fact that if structure is simplified by parasitic life, then physiological processes also must alter, for structure and function always go hand in hand. A change in the one means inevitable change in the other; and if in a free-living creature a number of organs are required to perform a certain number of functions, and one or more of these organs is removed or simplified, then the function it performed must either be taken on by the others or be performed in some other way. The end result in any event is that such vital functions as reproduction, digestion, respiration, excretion, and the transport of food and oxygen about the body and waste matter out of it, have still to be performed, but by fewer organs. The animal's physiological processes,

therefore, become more complex in the sense that they have to be effected with more economy of means.

How is respiration effected by the parasite, for example? The ectoparasite, living on the surface of either its terrestrial or aquatic host, is under no greater difficulty than its victim, and we do not find that its respiratory system undergoes any marked alteration as a rule. But the endoparasite, living in the alimentary canal or in the tissues, must somehow find and take in oxygen. In the tissues themselves, bathed as they constantly are by the lymph, a fluid whose function it partly is to carry the oxygen to all parts of the body, the parasite is lodged amid plenty. In the blood, likewise, the malaria parasite and the trypanosome have entered a medium which not only carries food in solution to the body, but oxygen as well. Even sarcoptes, the mite that causes scabies of man, burrowing deep in the skin, can get its oxygen through the small tube that it digs. But in the intestine, bathed by digestive ferments, acid, alkali, and the gases that the digestive process produces, how does the tapeworm or the entamoeba fare? This is a problem that still awaits clear explanation.

Such endoparasites as live in the stomach itself, such as the larva of the horse bot-fly *Gasterophilus* or the worm *Hamonchus contortus* that lives in the fourth stomach of the sheep, presumably can get enough of the vital oxygen from the air swallowed by their hosts with their food. The larvæ of the sheep nasal fly (*Estrus ovis*, which are laid by the adult two-winged female fly in the nostril of the sheep, and subsequently crawl up into the spaces in the skull behind the nose and set up serious inflammation there; or those, such as the larvæ of *Lucilia caesar*, the green-bottle fly, which may attack in a similar way the nose and ears of man in the tropics, often causing frightful sores and ulcers; or others, that may burrow under his skin (species of *Dermatobia*, *Hypoderma*, *Cordylobia*,

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etc.) or be deposited in foul wounds and live there much as blowfly maggots will live in decaying meat—all these are in sufficient contact with the oxygen of the air for their needs. But the means by which the gut parasite satisfies that oxygen hunger which is common to all living things has not yet been satisfactorily explained.

Experiments done by Weinland on the parasitic worms suggest a possible explanation. He found that these worms contain a much higher percentage of the starchy substance glycogen than do animals as a rule, and it has been suggested that such creatures may obtain their oxygen by the breakdown of this substance. If this is true, it is an interesting instance of the acquisition of a special physiological habit by a parasite as a direct result, we may suppose, of its parasitic life. Some of the special modes of feeding shown by certain of the bacteria may be examples of a similar adaptation along different lines.

We ought to remember, however, that some of the bacteria have developed a power of living without any oxygen at all. They are what are called *anaerobic*, some of them being incapable of living in a medium containing oxygen (obligatory anaerobes), and some able to live either with or without it (facultative anaerobes). Some of the parasites living in the intestines of animals may have acquired a similar faculty.

The blood and the system of tubes by which it is carried throughout the body of those animals which possess it must always be considered in relation to the respiratory system; for one of the functions of the blood is to carry to every part of the body the oxygen taken in by either the gills or the lungs, or by both. Any change in the method of taking in oxygen must therefore be followed by changes in the blood vascular system: and if creatures which possess a well-developed blood vascular system become parasitic to such a degree that their respiratory organs are pro-

foundly modified, the blood vascular system will be modified also. As a matter of fact, very few profoundly modified parasites are descended from ancestors with a well-developed vascular system. The insects, which do possess such a system, have not, as adults, at any rate, gone further than ectoparasitism, and we note in them, therefore, little more than a simplification of their blood vascular system if there is any change in it at all. The flatworms, which are most modified, come from ancestors which had not yet developed a vascular system.

It is, perhaps, significant that so few creatures with an efficient blood and channels for its transport have taken to the parasitic life. It may mean that the evolution of this blood and its system of transporting vessels conferred on its owner such a great physiological and evolutionary advantage that, like the vertebrate with its greatly superior organisation and control, it never experienced the need to explore such bypaths of life as the parasitic habit.

Excretion of waste, that other vital necessity of living things, presents no greater difficulty as a rule to the parasite than to its free-living relative.

But one other structural unit of the body remains to be considered, the most important one of all in some respects—the nervous system. What effects does the parasitic life exert upon that? We are still, of course, on the threshold only of our understanding of the nervous mechanism of animals; and the difficulties in the way of studying its operation in the parasite are very obvious. For to do this we must observe the animal in its natural surroundings, and we know as yet no way of reconstructing in the laboratory the interior, say, of a sheep's liver full of flukes, or the intestine of a man with tapeworms in it. But we can see certain obvious facts.

We note, as before, the loss of organs that become useless. Just as the eyes of the cave newt are covered

with skin, or those of the burrowing mole are reduced, so the eyes of a creature that takes to parasitic life tend to disappear. We can trace if we like a whole series of similar losses, a reduction and eventual disappearance of some organs that were essential to the free-living creature which needed to be very keenly aware by smell, hearing, and sight of all that went on around it. The same principle operates as brought about the loss of locomotor organs; and just as in that instance whenever the young stages of the parasite were still free living—as, for example, the young miracidium and cercaria larvæ of the liver fluke—the locomotor organs were retained, only to be lost when either that stage or the adult became parasitic, so the young phase of a parasite may have sense organs and lose them later. The same miracidium larva, for example, has two eyespots at the front end of its conical body; but the adult fluke has no eyes. Associated, perhaps, with changes of this kind in those parts of the nervous system concerned with the perception of light must be reckoned the loss of colour by such forms as the tapeworm, which, like the white cave newt, lives in darkness; and also certain resemblances in colour and pattern between ectoparasites and their hosts, which must be regarded as protective adaptation.

The nervous system itself is liable to disuse in parasitic life. Its primary function—to inform its owner of what goes on in the environment and to correlate the bodily activities, both internal and external, to those happenings—loses much of its value when any creature gives up active life or enters the body of another. But we ought to remember once more the points we made about the blood vascular system. The nervous system is less altered in the ectoparasite than in the endoparasite, and probably few parasites have had ancestors which possessed a really highly developed nervous system. Again, we note that the insect parasites were originally best equipped in this respect. The flatworms

never had more than a rudimentary nervous mechanism, the protozoa none at all. And perhaps it is also true that those creatures which did develop an efficient nervous system thereby acquired, as the vertebrates did, for example, so great a potential mastery of their environment that a free life of initiative and adaptation in the world outside never presented any serious difficulty to them. They could always find a corner in which to live and maintain their kind, so that even the bitter struggle for life could not force them to explore the ways of the parasite. It is not that they would have found an easier life if they had done this, for the parasitic life is by no means free from struggle; but no need arose to turn from the outer world.

We must not forget, however, that the parasite is exposed, no less than its free-living relative, to stimuli of all kinds that come from its surroundings. To exchange life in a pond for life in a gut does not mean freedom from prickings: and these it is the function of the nervous system to record. Thus to *tactile* stimuli parasites must be sensitive, to temperature changes they may be very sensitive, and above all things that influence the lives of parasites, especially those of endoparasites, the influence of chemical substances must be particularly important. Responses to these are called by the general term *Chemotaxis*. Upon them depend, perhaps, the often astounding and very complicated journeys made through the body by such creatures as the roundworm *Ascaris*, which will regularly leave the intestine where it is born and bore its way into the blood stream, by which it is carried to the liver. From there it is carried through the right side of the heart into the lung, and it then either crawls up the air tubes into the back of the mouth or irritates the lung so that it is coughed up. From the back of the mouth it then finds its way down the gullet into the stomach and so back to the intestine, where it grows up.

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Other journeys are still more remarkable. The young of the miner's hookworm bores through the human skin. By what means does it find its way through the maze of tissues and influences within the body to the small intestine which it must either reach or die? The minute sporozoite, not more than one four-thousandth of an inch in length, that is the earliest stage of the gregarine protozoan parasite *Monocystis*, which lives in the vesicula seminalis of the common earthworm, must enter its future habitat with the earthworm's food. Set free in the gut, it immediately bores into the tissues; and somehow it finds its way to those pouches in the ninth to the twelfth segments of the worm where its future life is to be lived. The eggs of the warble fly *Hypoderma* are laid on the hairs of a cow. Grubs emerging from them crawl down the hairs to the skin, bore their way through it with their strong mouth hooks, and for seven months wander about in the body of the cow, moulting during this period and growing to five times their original size. Then they find their way to a position underneath the skin of the back of the cow, cut a hole in this through which they may breathe, and, moulting several times, grow rapidly, feeding on the matter of the sore which they produce. Finally, they work their way out of the sore when they are full grown, fall to the ground, and seek shelter under anything available, and then become chrysalises, from which the fly emerges to start the same cycle again.

The mechanisms by which such amazing migrations as these are controlled are as yet unknown. But it is more than likely that a large part is played in them by what are called *Tropisms* of various kinds—that is to say, by regular responses by the creatures concerned to various stimuli from their surroundings.

Nor should we forget, when we are considering parasites, what Brumpt has called *Histotropism*—the attraction exerted by certain tissues of the animal body

for certain parasites. The entry of the young forms of the hookworm into the skin of man, or that of the larva of the warble fly into the ox's skin, may be so caused, as may be also those instances of the migration of a parasite to a particular tissue such as the "preferences" for certain parts of the body mentioned in Chapter IV. But to call such phenomena instances of histotropism does not, it must be confessed, explain very much. We are as far as ever from really understanding how they are caused. It may be that these journeys are nothing more than the normal escape of the creatures concerned from environments that are unsuitable to them; but such a simple explanation will not account for the regularity with which they are carried out, nor for the remarkable accuracy with which the parasite reaches its proper destination. The truth is that we know very little about these matters at all.

CHAPTER VII

ADAPTATIONS OF THE PARASITE TO ENSURE ITS SURVIVAL

THE reproduction of its kind, dispersal of them over the earth, and the adoption of various means to ensure the survival of its species, are, perhaps, the most fundamental instincts of every animal; and the operation of them in the parasite must now be considered. To the power of their influence must be ascribed that remarkable feature of all parasites, the size and complexity of their reproductive organs. Their other organs may be simplified or lost as a result of parasitism—almost every other structure of the body may, as we have seen, be discarded—but the genital glands remain; and whatever the degree of modification in them, it is more marked, as it is in other structural features, in the endoparasite than in the ectoparasite.

One reason for this increase in size and complexity of the reproductive organs can be seen when we inquire why it is that the parasite can produce as a rule many more eggs and sperms than its free-living relative can. The number of eggs produced, especially in instances of advanced parasitism, is astounding. It has been calculated, for example, that *Tænia solium*, the pork tapeworm of man, can lay forty-two million eggs; that *Ascaris lumbricoides*, the common roundworm of the pig, can lay as many as sixty-four millions; and that *Tænia saginata*, the beef tapeworm of man, can produce one hundred and fifty millions. Such remarkable fertility may be compared with that of the lower vertebrates such as the fishes, and may be equalled also by animals that lead a sedentary life; and in all these instances the reason for it is the same.

Both eggs and young, defenceless embryos are con-

stantly being destroyed by other animals which regard them as attractive titbits, and by such adverse influences as drought, heat, and frost. For the parasite there is the further problem that its young must find its right host, or more than one such host. The dice are thus heavily loaded against all eggs and embryos that are not under parental care, and to meet these odds large numbers of young are produced so that the greatest possible number may survive. Conversely it is true that, when parental care confers upon the offspring, and through it upon the species, a great advantage, as happens among the four-footed, hairy, hot-blooded mammals which suckle their young, then the number of eggs produced by the female in her lifetime is relatively smaller, and the number actually fertilised perhaps smaller still. We can state it as a general rule, therefore, that in the animal world the number of eggs produced is directly related to the chances of their subsequent survival, although to this, as to every other biological law, there are exceptions.

Not all parasites, for example, rely upon mere mass production of eggs as a means of improving their chances of survival. Eggs have to be fertilised as well as laid; and this may be difficult for the parasite to accomplish, especially if, as so often happens, the locomotor organs have been lost or reduced. The sedentary animal has the same difficulty, and neither it nor the parasite can rely, as can the equally immobile plant, upon the chance that other animals will transfer its sperm to the egg. Some parasites have, therefore, like some sedentary animals, adopted means of making fertilisation easier.

The two sexes may, for example, become more or less permanently associated. The fluke *Schistosoma* (*Bilharzia*) is an example of this. Though the sexes of this worm are separate—it is one of the exceptions to the rule of hermaphroditism referred to below—the male worm folds over the edges of its flattened body

to form a groove in which the longer and cylindrical female usually lives. A more advanced instance is the roundworm *Syngamus trachealis*, which lives in the windpipe of chickens and other birds, causing the disease called gapes with its constant yawning and outstretching of the neck. This is another unisexual species, and the smaller male is permanently attached to the female at her genital opening, the two together forming a Y-shaped individual. Of a different kind is the association of males and females shown by the whipworm *Trichosomum crassicaudum*, parasitic in the urinary bladder of the rat, the female of which keeps two or three males actually inside her uterus. The small males of the parasitic crustacea, referred to in Chapter V., and those of the curious fishes *Photocorynus spiniceps* and *Edriolychnus schmidtii*, are examples of another means still of ensuring the fertilisation of the eggs, for the males of these species have become parasitic on the females, a condition of things that is not unknown in human society, and their structure has suffered accordingly.

Another and more efficient method of attaining the same end is the complete abolition of the distinction between the male and the female and the production in one and the same individual of both eggs and sperms. This is called *hermaphroditism*, and it is worth noticing that, just as the sedentary animal often shows the simplification and loss of structural features so common in the parasite, so it is also often hermaphrodite. This fact, that the parasite and the sedentary animal continually remind us of each other, is important. It means, not that the one is necessarily related to the other, but that the parasitic life approaches the sedentary state and produces like results. Any resemblances between parasitic and sedentary creatures are therefore due, not to genetic affinity, but to the influence upon different stocks of similar ways of life, a principle which the biological philosopher calls *Convergence*.

The extent to which hermaphroditism has been adopted by parasites is remarkable. It is one of the reasons why their reproductive organs are so bulky and complex, and the causes of it are not confined to the need for easy fertilisation. For hermaphroditism does not necessarily mean self-fertilisation. It is possible that this is effected by some of the liver flukes, but cross-fertilisation is the rule, and perhaps this is imposed by the laws of evolution as a necessity if a vigorous stock is to be maintained.

The tapeworms, each segment of which contains both male and female genital glands, present a special difficulty in this respect, for it is not easy to decide whether each of these segments is to be regarded as a separate individual, or whether the whole worm is the individual and each segment a part of it; but the fertilisation of the ripe eggs in any one segment by the sperms also produced by that segment is prevented by the fact that the sperms are developed first and the eggs ripen later, so that any one segment rarely contains both at the same time. The eggs in each must therefore be fertilised by the sperms of another segment, and the movements executed by the worms in the intestine are doubtless due in part to the efforts of the segments to approximate themselves to one another for the transference of sperms.

If the normal processes of sexual reproduction may thus be modified by parasites to their own benefit, these are not the only means at their command of improving their chances of survival. They can also multiply their numbers at some stage or other of their life history by some form of asexual reproduction. From the egg of the common liver fluke of the sheep, for example, emerges a microscopic ciliated larva, which, after a free life in a pond or a ditch, bores its way into the snail *Limnaea truncatula*; and inside the tissues of this snail it becomes a little sac called a sporocyst, from the walls of which a generation of small tubular

organisms, each with a blind intestine, develop. These are called rediæ, and they also bud off from their interior other rediæ. A fourth generation arises from these in a similar way, but this is different. It is called a cercaria, and it has a minute oval body with a forked blind intestine like that of the adult fluke, and a tail by means of which it can swim in ponds and ditches after it has left the snail. Its business is to find its way to the alimentary canal of the sheep; and it does this by swimming to the margin of the pond or ditch, wriggling up the banks and on to the grass of wet pastures. There it forms round itself a hard case which protects it from heat and drying, and in this it awaits the moment when the sheep crops the herbage. Once inside the sheep's stomach, it leaves its case, finds its way to the bile ducts of the liver, loses its tail, and grows up into the adult fluke.

Such a life cycle gives some idea of the odds against the survival of a parasite. If the miracidium does not meet with a snail it quickly dies. Moreover, it can live in one particular species of snail only and must find a member of that species. Even if it finds the right one and multiplies in it, the cercaria that emerges again may die before it reaches the pasture; or if it reaches the grass it may not be eaten by a sheep before it dies; or some other herbivorous animal whose digestive juices it cannot resist may swallow it. To meet these odds the parent fluke produces great numbers of eggs in the first place; and each of the embryos emerging from this is again multiplied by the generations produced asexually in the snail. Such multiplication by a larva by asexual methods is called *pædogenesis*.

We see it also in the cystic stages of such tapeworms as *Tania cœnurus*, which causes the disease called staggers or gid in sheep, and *Tania echinococcus*, which may cause hydatid disease in man. In these instances the parent worm produces its eggs in the ali-

mentary canal of a vertebrate host. *Tænia cœnurus* lives in the gut of the sheep dog and other dogs. Its eggs, passed out with dog's excreta, lie on the pastures and are eaten with the grass by the sheep. In the sheep's intestine a small embryo emerges from them which bores its way through the wall of the gut and gets into the blood system. By the blood stream it is carried all over the body, and, reaching the smallest bloodvessels or capillaries, passes through their delicate walls and makes its way into the surrounding tissues. Here it settles down; and in this particular species it develops best in the nervous system. If it lodges in the brain, for example, it grows into a small bladder full of fluid sometimes called the *Cœnurus*, and as this increases in size there appear on its inner walls small buds which are really the heads of tapeworms turned outside in, each of them complete with the typical four suckers. Hundreds of these may be formed, and they cannot develop further unless they are swallowed by a dog, in whose intestine they grow up into tapeworms again.

From the parasite's point of view, therefore, the best result of the disease caused by the pressure of the cyst is that the sheep should die, or be killed by the farmer and its head thrown away; and this actually happens on farms where the farmers are careless or ignorant of the parasite's life history. It would also happen in a state of nature, where the sheep would either die or be killed and its carcase, including the head, would be investigated and eaten by dogs or, in the wild nature of earlier times, by wolves, and with it the cyst would be swallowed. In this way a dog may infect itself, even by devouring a single cyst, with hundreds of tapeworms.

Tænia echinococcus is another tapeworm which multiplies its numbers inside a cyst full of fluid. It also lives in the dog's intestine, and its eggs may be swallowed by human beings who eat raw vegetables or salads which have been fouled by the solid excreta of infected dogs. If this occurs the embryos emerging

from these eggs may find their way to the liver of man and there give origin to a cyst even bigger than that produced by the young of *Tænia cœnurus*. On the inner walls of this bladder, not only the heads of potential tapeworms may develop, but also daughter cysts. These daughter cysts may even give rise to granddaughter cysts, and in both of these many tapeworm heads may appear, so that in the whole cyst there may be enormous numbers of potential tapeworms. Such a cyst is called by the doctors a *hydatid cyst*, and it may reach the size of a baby's head and cause, like the similar cysts mentioned in Chapter IV., very serious trouble by pressing on the liver, the lung, the intestines, or important nerves or bloodvessels in its neighbourhood. But otherwise it is usually harmless. The tapeworm heads inside it cannot develop further in the human body. They can only develop if the cyst is eaten by a dog, so that it is certainly a calamity for the tapeworm if its eggs are nowadays eaten by a man. If any other mammal swallows them, there is, of course, more chance that a dog may eat its carcase and so enable the thousands of heads in the cyst to grow up into tapeworms again.

Both these instances are examples of larval multiplication called *pædogenesis*, and the total effect of both this and the enormous numbers of eggs produced is to counteract the difficulties to which the parasite's complicated life history exposes it and to increase its chances of survival.

Most other tapeworms rely upon the large number of eggs alone. Each egg, for example, of the pork tapeworm of man gives rise, if it is taken in by a pig, to an embryo which grows into a cyst in the muscles of the pig, but this cyst contains only one small tapeworm head. If a man eats raw or insufficiently cooked pork containing such cysts, from each a single tapeworm will emerge, but only one. This may seem to lessen the chances of the pork tapeworm's sur-

vival, but we must remember that carnivorous animals do not cook their food, nor did man before civilisation and such influences as the Mohammedan or Jewish religions began to interfere with Nature's ways.

We may sum up the matter by saying that to meet the chances against its embryo ever getting into the second host in which it must live part of its life, the tapeworm produces enormous numbers of eggs; and to meet the chances against its ever getting out of that second host again and back into the right first host, the *cœnurus* and the hydatid cyst have been developed.

Among the parasitic members of the *Hymenoptera*, the group of insects to which the ants and bees and wasps and sawflies belong, there is another method by which the offspring may be multiplied, a method which is called *polyembryony*, or the production of more than one embryo from each egg. The egg of *Ageniaspis* (*Encyrtus*) *fuscicollis*, for example, which is parasitic on the injurious small ermine moths of the genus *Hyponomeuta*, undergoes a kind of budding to produce a row of embryos enclosed in a tube, all of which may ultimately grow into adults. This also can be considered as a means of increasing the chances of the survival of the parasite.

Under this heading also we should, perhaps, include *parthenogenesis*, the development of offspring from the unfertilised egg. For it is quite evident that if the egg need not be fertilised, one important category of menaces to survival—namely, all those influences which prevent the union of the adult sexes—may be avoided. A few parasites, such as the tick, *Amblyomma agamum*, and some of the parasitic *Hymenoptera*, show no other method of reproduction. In other instances, such as the various species of greenfly that show it, parthenogenesis occurs only in the spring and summer, and the onset of winter determines the production of a male and female generation.

CHAPTER VIII

ADAPTATIONS OF THE PARASITE TO ENSURE ITS SURVIVAL (*Continued*)

AMONG the adaptations which help the species in the battle for survival we must also reckon those powers, possessed by the young stages of many parasites, of resistance to such inimical climatic factors as heat, frost, and drought. The embryo is often the most vulnerable phase of an animal's life, even when that animal is accustomed to the battle of life in the outside world. The ectoparasite is, of course, still exposed to a large extent to the rigours of this physical world, so that we find that its young stages are not very different from those of other free-living animals. But the endoparasite, accustomed to life inside another animal, must make some provision for its young if they have to leave the shelter of the host, and, for a while at least, live outside it. This provision usually takes the form of some kind of protective envelope, like that, for example, which encloses eggs, or the hard wall or *cyst* in which are protected the germs of the amœba which causes dysentery. Such cysts are always produced by those parasites which, without any effort on their part, reach their host by what can be called the *contaminative method*—that is to say, by the contamination of the host's food and drink by these resistant phases.

From the eggs of most parasitic roundworms, for example, such as the one which lives in the fourth stomach of the sheep, an embryo emerges which, after one or more moults, may remain enclosed in the dried and thickened last skin that it sheds, and thus may resist for long periods the rigours of climate that pass across the pasture on which it lies. The powers of re-

sistance of some cysts of this sort, and also of eggs, are very remarkable, and they are important aids to survival. It is often essential, moreover, that such resistant phases should lie thus outside the host for a certain period, because usually the embryo of a parasite cannot infect a new host until it has undergone definite biological changes which result in its becoming "infective"—that is to say, able to infect a new host.

The necessity for such power of resistance to rigours of the external world is greatly lessened when a parasite adopts a second host as well as a first one. An example of this was given above when the life history of the liver fluke was described. Two facts will be noticed about it. First, that the egg of the fluke has to suffer far less life in the outer world, because part of its life history is passed inside a snail; and, second, that it cannot infect another sheep until it has passed through a biological cycle in a particular species of snail—namely, *Limnaea truncatula* in this instance.

The young of the broad tapeworm of man, *Dibothriocephalus* (*Diphyllbothrium*) *latus*, must even pass through the so-called water-flea, cyclops, and a fish which swallows this, so that three hosts are required.

When parasites thus live inside the bodies of two or more hosts instead of one, and are alternately passed from one to the other, we speak of an *alternation of hosts*. The host in which the adult stage of the parasite lives and in which sexual reproduction takes place if it occurs inside the host at all, is called the *definitive or primary host*; that in which other phases of the parasite live and in which asexual reproduction may occur is called the *intermediate or secondary host*. Thus the primary host of the common liver fluke, *Fasciola hepatica*, is the sheep or some other mammal; and its intermediate host is the snail *Limnaea truncatula*. For other species of fluke the species of snail that can alone act as their intermediate hosts is different. Many other parasites are in a

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similar way restricted to only one species of intermediate host, so that one of the problems of their life-histories is that they have to find this particular species of animal and enter its body; for no other species will do, not even nearly related species of the same genus. Less commonly parasites are restricted also to a single species of primary host. The tapeworms, *Tania solium* and *Tania saginata*, for example, can live in man only; and repeated attempts to rear them in the dog, which is such a favourite host of the tapeworms, have failed completely. *Tania crassicolis* adheres to the cat very closely, and *Trypanosoma lewisi* to the rat. Most trypanosomes, on the other hand, can live in the blood of more than one species of vertebrate, and the same is true of many parasites with both primary and secondary hosts.

Parasites which are restricted to one species of either primary or secondary host, or of both, are obviously at a disadvantage, for their close adaptation to these hosts not only makes it easier for us to control them, but also increases the difficulty the parasite always has of finding its right host. This difficulty is increased when the parasite does not pass, as the liver fluke does, part of its life inside its two hosts and part in the outside world, but lives the whole of its life inside one or other of its hosts and never enters the outside world at all. Such a parasite does not need to make protective cases for any stage of its life history; but, although it benefits by the continuous shelter provided by its hosts, this benefit is neutralised by the fact that it is now entirely dependent upon these hosts. Further, it is usually conveyed from one to the other of them passively and has paid for its shelter by loss of the power of entering either host by an active effort of its own.

Consider the protozoan parasite, *Plasmodium*, which causes malaria in man. It lives in his blood, and this blood is sucked up by a mosquito, in whose stomach the males and females only of the *Plasmodium* survive

the action of the mosquito's digestive juices. They produce in the stomach male and female elements which unite to form a fertilised egg, or zygote, and this becomes itself parasitic on the wall of the mosquito's stomach, growing there in the form of a soft-walled cyst, inside which countless small germs called sporozoites are produced. This cyst then bursts into the mosquito's blood, and by the blood the sporozoites are carried to the spittle glands, and from them are injected back into the human blood when next the mosquito bites a man.

The trypanosome that causes sleeping sickness in man has a cycle that is similar in principle. It lives in the blood and cerebro-spinal fluid of man and is taken up by the bite of a tsetse fly, in whose intestine it undergoes a definite biological cycle, and until this has been completed it cannot again live in human blood. That infections of man do occur without the completion of this cycle is quite true. Tsetse flies, immediately after they have taken up trypanosomes, may again bite a man while their mouthparts are still wet with the blood of their first bite in which blood trypanosomes are swarming. Such *direct* transmission has been responsible, in part at any rate, for epidemics of sleeping sickness in Africa; but it is nevertheless exceptional and the rule of *indirect* transmission after a definite cycle has occurred in the fly, still holds.

Yet another example of this kind of life history is that of the flagellate protozoa of the genus *Leptomonas* which have not adopted an animal, but plants of the group *Euphorbiaceæ*, as their hosts, in the latex of which they live and into which they are injected by the bites of hemipterous insects or bugs which suck the juices of these plants.

Examples could be multiplied: but enough have been given to emphasise the increase of difficulties before the parasite which, like the ones just cited, must not only go through a biological cycle in the

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second host as well as in the first one, but must also rely for transmission on the *inoculative method* by the bite of some other temporary ectoparasite which conveys them as passengers which make no effort on their own behalf.

That such difficulties are real is proved by the fact that some of these parasites have evolved what must be regarded as a means of counteracting them. If they do not multiply in their larval stage as the liver flukes do, they can multiply their numbers by a series of generations produced by the asexual method of division into a great many parts. This division occurs, for example, fairly regularly at intervals of three days in one species of the malarial parasite of man, and to it is due indirectly the regular attack of fever characteristic of that disease.

Such asexually produced generations, however, are usually the ones that cause the damage that the parasite does, and they may increase the numbers of the parasite to such an extent that the organ in which it lives is completely overrun by them, as the intestine may be overrun, for example, by the protozoan parasite that causes a form of white diarrhoea in poultry and cattle and other animals. The damage done thus may be so great that a violent diarrhoea results, by which many of the parasites are swept to certain death in the world outside, or the host is killed, and with it all the parasites in it, so that all the advantage gained by increase in numbers is neutralised, at any rate so long as the host remains susceptible or ill-adapted to the parasite's effects upon it.

We can further realise the actuality of this risk for the parasite of non-transmission to its primary host if we consider what has happened to the malarial parasites of man which were injected by mosquitoes during the war into many English soldiers in the East. While the soldiers remained abroad the parasites found no difficulty in completing their life cycle. Mosquitoes

bit Tommy Atkins freely and took up parasites from his blood, harboured them in their bodies until they produced countless sporozoites, and injected these again into the soldiers. Thus malaria spread and was able, notably in East Africa, to put whole battalions out of action. But in course of time these battalions were sent home to England; and in most parts of England there were no mosquitoes to bite the men and enable the parasites to develop. In some parts of England, it is true, there were; and there was for a time a real danger that these mosquitoes, which were until then clean of the malarial parasite, might take it from these men and so become capable of passing the disease on to other English people. But that danger is practically over. Most of the mosquitoes of England were not of the right kind, for fortunately the malarial parasite cannot develop in every kind of mosquito. It has become adapted only to life in certain species of mosquito, and where that species does not exist the parasite cannot live nor the disease occur. Not only this, it is confined only to the females of this species, for the female mosquito alone is a blood-sucker, the male feeding on the juices of plants.

The same close adaptation to a particular kind of intermediate host is characteristic, though less strictly, of the trypanosomes that cause sleeping sickness. These parasites, in the course of a long life of parasitism, have acquired the power of living harmlessly in the blood of the antelope and other big game and domesticated animals of Africa; and from this they are usually taken up by the tsetse flies, pass through a definite cycle in the intestine of these flies, and are injected back again. Where the tsetse fly does not or cannot live, therefore, these particular trypanosomes cannot live either, so that the distribution of the one corresponds exactly to that of the other. If we could remove the fly we could destroy the trypanosomes: and the same result would be obtained by the destruction of the

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mammals which harbour these tyrpanosomes in their blood. The latter expedient has actually been proposed, though it is scarcely practicable; and, as Professor Duke has recently pointed out, to remove these animals from the vicinity of man simply means that we remove the normal food supply of the tsetse fly and so provoke it to bite human beings and infect them. An increase and not a decrease of sleeping sickness would therefore follow.

Such parasites as these just mentioned must be regarded as much more advanced in parasitism than, say, the liver fluke or the tapeworm, because they have lost the power of living outside a host of some kind. They are, therefore, entirely dependent on their hosts, and frequently need particular species of such hosts or even, as in the instance of the malarial parasite, the females of it only. The malaria parasite, indeed, boxed up as it is in the blood of, say, an Indian soldier, is like a prisoner in a well-guarded dungeon. It can live there, it is true, for very long periods, perhaps throughout the life of the soldier, but only a certain female can let it out, only the female of a certain kind of mosquito; and it must rely on her hunger-instinct for deliverance.

The adoption of a second host cannot, therefore, be regarded as always advantageous to the parasite. It is doubtful whether it reduces or increases its chances of survival. But we must remember always when we reflect about such matters as this that the parasite has no choice; it is driven by the law of the survival of the fittest and by whatever other evolutionary factors biologists may yet discover.

We cannot say yet how the malarial parasite first acquired the habit of passing part of its cycle in the mosquito. Authorities have so far failed to decide with unanimity whether it began first in the mosquito or in the blood of man. It is certainly hard to understand how a small and very delicate amœba like

the malarial parasite could have begun its parasitic life in human blood. How could it have got there in the first place? But if it was originally a parasite of the insect, it is easy to understand that some parasites could have been injected into human blood when the insect sucked that blood, and in that way entered man. Originally most of the parasites thus injected must have died, being killed by the marvellous power of the blood to battle with and destroy any foreign invader. But even if the early invaders were killed, some of those subsequently injected might survive; and they would cause a reaction of the man infected which would take the form of fever and the other manifestations which we call malarial fever or ague. That parasites still cause this reaction—this attempt of the human organism to rid itself of the parasite—means that the parasite has not yet adapted itself completely to life in man. For it is obvious that it is to its advantage not to cause such a reaction, but to live in harmony with him as it does with the mosquito in which we may suppose, because it causes no apparent disease of that insect, it has been parasitic for a long enough period to enable it to become completely adapted.

The still more striking instance of the *Trypanosome* supports this theory further. Whether these minute and beautiful ribbons of protoplasm moved by a long and exceedingly delicate whip were originally parasites of the digestive tract of the tsetse fly or of the vertebrate blood cannot yet be decided. But certainly some of them seem to have begun in their invertebrate hosts. If we take the one that causes the disease called nagana in cattle as an example—namely, *Trypanosoma brucei*—we know that it passes part of its cycle in the gut of the tsetse fly, *Glossina morsitans*, living there in perfect harmony with the insect and causing no disease. It can also live in other species of biting fly. So that its chances of transmission from vertebrate to vertebrate are greater than those of the malaria parasite.

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Moreover, it is less rigidly adapted to particular species of vertebrate host, for it normally lives in the blood of several kinds of wild ungulates in Africa and causes in them no disease. But if a tsetse injects it into the blood of domesticated cattle it causes in them the disease called nagana. It is, in other words, not yet fully adapted to life in the domesticated cattle; and injection into them is, without doubt, a calamity for it, for it must result in the sickness or death of the cattle, which means that many or all of the parasites in them are destroyed. If this parasite is injected by the tsetse fly into man, as has happened in Rhodesia, the result is still more calamitous for the parasite. It produces in man a very severe and often fatal form of sleeping sickness, which must result in the death of great numbers of the parasite.

The fact that this particular species of trypanosome has comparatively recently acquired the power of living in the blood of man is obviously an instance of a parasite in the early stages of adapting itself to new vertebrate hosts. In course of time, we may be sure, man will suffer less from this kind of sleeping sickness, partly because he will adapt himself to it and partly because the parasite will adapt itself to him. There will thus very slowly arise a state of affairs like the greater tolerance, as we say, of the African native to the ordinary form of sleeping sickness caused by *Trypanosoma gambiense*. The native suffers from it less than the white man because he has had longer time in which to try to adapt himself to it, and the parasite has also had longer time to grow accustomed to life in the native's blood. The malarial parasite has approached even nearer to that state of mutual tolerance between host and parasite which is the parasite's ideal, for we might almost say that nearly every native in some parts of the tropics has had malaria in youth and tolerates it throughout life without such serious effects as the white man, less used to it, must suffer. *Entamoeba*

histolytica, which causes a human dysentery, shows an even closer adaptation to its host, for it has been calculated by Dobell that seven to ten per cent. of even the population of England harbour this parasite. It is constantly doing minor damage to them, but that damage comparatively rarely amounts to the proportions of a disease. The percentage in tropical countries is much higher. It is easy also for anyone with a microscope to discover that in such countries as China and Arabia, where food is frequently contaminated as a matter of course or policy by human and animal manure, almost every individual harbours worms of various kinds in his intestines. Yet such is the natural balance between worm and host that most of these individuals are healthy enough.

Such facts as these teach us that the opinion so often expressed that a parasite is always dangerous is not correct. If we look at it as the human being naturally does, as an unclean invader of our bodies, and of the bodies of other animals, we must take such a view. But if we see it as we ought to try to see it, from its own point of view, we shall get a truer conception and shall realise that it is to the very great disadvantage of a parasite to cause disease in its host. For disease means reaction against it. The two terms are synonymous; and even the human being parasitic on his own community is wise enough to see that to provoke such a reaction is very foolish.

The fact remains, however, that the parasite does cause disease. It does so when it first explores new hosts, and it may not survive such attempts to conquer new pastures. It also causes disease by lowering the resistance of its host to other parasites. A man full of tapeworms, a lamb with a hundred and twenty feet of the tapeworm *Moniezia* stealing the food from its intestine, are not in good health, although these particular parasites may not be hurting them to the point of sickness. But their strength is lessened, and other

parasites, especially the bacteria, may overcome them then. Whether the parasite or the host wins will depend upon the reserve strength of either; and that in a nutshell is the secret of all recovery from disease.

We have learnt, then, that equilibrium between the parasite and the host is the best for both: that the parasite does not always cause disease, though it always does damage; that it does most harm when it first attempts to adapt itself to a host it has never entered before; and that, whatever the equilibrium that is eventually established between the two, this is always liable to be upset by any sort of influence, whether it be another parasite, a mineral or animal poison, or a sudden change of temperature or other effect of the environment, which lowers the general health of the host. Such disturbance of the equilibrium usually damages the parasite, for if it takes the form of an increase of the host's resistance, the parasite must find it more difficult to live, and if it is affected by the host's loss of health the parasite is generally destroyed in great numbers. And in taking this view we have tried to avoid the common error of attributing a knowledge of purpose to the parasite. It has not adopted the parasitic mode of life from choice. Unlike the human "sponge," it could not say to itself: "Here is a way, with the sacrifice of some independence and honour, of having an easy time in a bitter world." If it could have thought so, it would have been quickly disillusioned, as the preceding pages must have shown. Nor does the parasite know that it is to its detriment to kill or cause disease in its host. It is more like the wild cat that will kill all its food supply from sheer lust of blood and then starve; and it may be that some of the elaborate reproductive adaptations shown by parasites, and, indeed, by all living things, are Nature's way of guarding against this repercussion of her law that the animal, for reasons given in the first chapter, must kill and eat. To breed and propagate the species is another

primary need of living things, and usually this predominates. But the former may go near to the extermination of all food and so prevent the possibility of the latter. This is so, we must believe, only when the balance that Nature insists on in the long run has been upset. Ultimately, given the time she so generously allows herself, she works back to an equilibrium that gives a fair chance to all.

Arguing thus, we may feel a sudden qualm, for is not such a theory merely another example of that almost inescapable bane of ours, the human point of view? We will, as men, to be just; and we speak of laws and fair chances and enough for all. But what do we mean when we speak of Nature's laws in this sense? Do we mean just ourselves?—that we are judging parasites by human standards and cannot understand why a trypanosome, for example, should be such a fool as to multiply to such an extent that it kills both its host and its progeny? The truth is that, given conditions that are sufficiently favourable, it will do so; instinct, the blind urge of sex, or the force of some biological cycle pursuing its inevitable course, sweep it on. Just as the law of increasing size led the ancient reptiles to extinction, so these other laws can lead the parasite to self-destruction from which nothing has the power to save it, except a like reasonless reaction of its host against it, or the conflict of the demands of other organisms with its own, or, latterly, what is a special instance of the same thing, the interference of man for his own ends.

CHAPTER IX

CONCLUSION

THE foregoing pages may have made clear the fact that if we wish to control or eliminate those animals which attack our bodies, damage our crops and domesticated animals, render unfit for consumption our stores of both animal and vegetable food, or destroy our clothes and fabrics and other manufactures, we must try to understand their whole life histories, so that we may strike at the weakest point in them. We can only do this if we study other animals as well as parasites, and we shall often find that the young stage of the parasite is the most vulnerable and that a "massacre of the innocents" is our cheapest or our only policy.

There will always be people who will object to any measure of this kind, for the simple if indefensible reason that they cannot approve of the destruction of any kind of life; and others, too, whose laziness or carelessness or lack of a sense of public duty leads them to shut their eyes to the miseries and hurt caused by parasites to man and other animals. The health of the public, the privilege of man to aid Nature in the task of creating and maintaining sane spirits in sound and vigorous bodies throughout the world—these are nothing to them. Others still, more subtle in their reasoning, may loose ironic shafts at the man who naïvely says: "This creature harms us, *therefore* we must exterminate it"; or, "This creature does us good, *therefore* we must foster it by every means in our power." For to argue so, they no doubt rightly point out, is to yield to the voice of the age-old instinct of self-preservation, and we ought by now to have conquered such primitive urges.

Yet the clever sophist can maintain with just as

much plausibility that most of the so-called "higher" ideals that modern man is supposed to have set up in place of the ancient gods of sex, hunger, and fear, are little more than tinsel we like to make for the decoration of our habitual garment of self-esteem. Our Truth, our Beauty, our Goodness and Benevolence, what permanence have they? If there come upon us a war or a famine, an epidemic of disease that decimates the human population, or any other catastrophe that wakens to action that terrible lion the primitive urge towards the preservation and propagation of the species, where are the altruistic virtues then? Brute force, blood lust, the ruthless destruction of all that harms or can harm us—these are our virtues when we are gripped by race fear. How, then, can we count ourselves "higher" or better than the tapeworm? That creature steals its host's food and selfishly strives, at the bidding of what we call Nature, to come to a working arrangement with its host. Are we its superior when we exterminate rats, or massacre mosquitoes wholesale, or gravely regret that we know no way of wiping out all the wild game of Africa because in their blood there lives, without harm to any but ourselves and the animals we wish to utilise, a tiny trypanosome that kills our best beloved?

We have a thing called a brain, that is all the difference. It gives us enormous advantage over other animals; it gives us choice also, which is denied to the parasite; and of that power of choice is born another self whose voice reproaches us when we wilfully kill and notice that the parasite cannot choose but to do harm. To still this uncomfortable voice we say, "Well, we are but human," meaning, though we know it not as a rule, that we are but animals still and must preserve ourselves as the tapeworm must.

Heart-searchings such as these are not, however, within the province of the practical biologist. If anyone shall ask him to tell how to control any animal

scourge, it is his duty, whatever his personal religion or philosophy, to give of his knowledge in a practical form; and no biologist will be slow to do this. The only lack is an adequate realisation by those in high places that biologists can be of real service to the community. There are signs that this serious defect is being remedied. We may hope that a competent biologist will be given both the position and the power demanded by his capacity to help all kinds of health worker, farmer, and educationist, to mention only three of the fields in which he can be useful. But for how long must we wait until this obviously necessary measure is taken?

It would be interesting, had we the further space, to consider several other lessons that the study of the parasite can teach us. They are lessons that are also taught by the study of any branch of biology; but parasitology especially brings home to us the need to avoid at all costs, if we wish to understand the animals aright, the prejudices that our human outlook is apt to create. When we study parasites we must guard, for example, against the human abhorrence of the principle of conduct implied by parasitism. We naturally dislike the human "hanger-on" or the man who "sponges" on others; and this dislike may blind us to other qualities he may have. It is not very difficult to carry this prejudice into the study of the animal parasites and to forget that our business is not to judge it by human ethical standards, but to see it dispassionately in the cold crucible of logic and to try to understand it as an intricate whole in relation to an intricate environment. To do this we must try to put ourselves in its place as far as we can, make an effort of imagination as well as of analysis and keep ourselves out of the picture. This is, in essence, what the great artist does when he studies the human material that he uses, and the attempt to do it must make us, not only better biologists, but also better men.

We must guard, too, against the human instinct to misunderstand the ugly. Great artists, great writers, men who are swayed by a sweet and revealing genius of pity, have overcome this prejudice against the ugly and have given it its due. But can even they without effort regard the tapeworm without loathing?

This means, if we look closely into it, that we feel, whatever we may be thinking, that the parasite is not only ethically ugly, but that its structure also violates our sense of beauty. Yet if that is the view of most people when a mass of lice in the hair of a child is being looked at, what is their view when they see a louse through a microscope and do not know what it is? Is it really the parasite that we feel to be ugly, or does its ugliness spring from the feelings we associate with it?

This is the same problem as the common prejudice against the painting or the description in words of, say, unpleasant industrial or slum conditions of life or the uglier passions. Yet it needs but a painter or writer of sufficient art, and we see a great beauty in what before was ugly. The microscope or the laboratory technician can perform the same office for us, and can do it without the artist's necessity of selection. They alter nothing, suppress no fact, but merely present the parasite as an animal stripped of its human associations; and behold! a liver fluke is a marvel of beautiful structure, a trypanosome a miracle of lovely sinuous movement in a drop of blood, and even a scab mite a thing of considerable beauty.

The parasite, therefore, is a living arbiter in the perennial struggle over that ancient bone: Is beauty in the object or in the observer? It proves the latter view to be right; or at least it works in favour of Alexander's view that "even natural beauty is a fusion of the object with the observing mind." For there can be no proper appreciation of the whole content of beauty in any object without a full knowledge and under-

standing of that object. When I see a tapeworm for the first time I may hesitate to call it beautiful; but the parasitologist who approaches it with imaginative sympathy, and has his wide knowledge of animals in general by which to judge it, may see that it has a beauty in its own category.

He will see, moreover, that, apart from the element of mere structural beauty in it, there is in every parasite a subtler beauty which only knowledge can reveal. Parasites, no less than other living things, are marvels of adaptation to the surroundings in which they have to live; if they were not they would not be able to live. Their slow evolution throughout the ages is a wonder awaiting whatever artist shall think he has the power to depict it; their fertility, the feats of food-getting that they perform, their incessant battle against heavy odds for the vital oxygen, and their struggle against innumerable forces that combine to destroy their young and do not cease their antagonism when those young that survive have grown to maturity; all these have the beauty that the human mind attaches to all things that invite, or even force, its admiration, or tickle its sense of romance, or show it, even in the life-struggles of creatures that it instinctively abhors, clear evidence of the existence of that guiding power which some call "élan vitale," or "nature," or "entelechy," or any other evasive name; but which some contentedly and frankly recognise as the spirit of God.

The conclusion, therefore, must be that whatever the angle from which we see the parasite, whether we be priests or artists or scientific observers, we cannot say that it is wholly false or ugly or evil. Our enemy it may be often enough; the enemy of all that lives, no less; but it is of our blood and our ancestry and kindred, and we can, if we will but honestly try to understand it, see in it grains at least of the truth, the beauty, and the goodness that are never absent from any constituent of our universe.

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FUNGI

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FUNGI

AN INTRODUCTION TO MYCOLOGY

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British Museum (Natural History)



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FUNGI

CHAPTER I

INTRODUCTION

WHEN studying living organisms it is customary to divide them into plants and animals. The acceptance of the usual ideas of evolution and the belief that life on the earth was first displayed by extremely simple organisms, carries with it the suggestion that these were neither animal nor plant, but partook of the characters of both of these divisions. The development of the green colouring matter, *chlorophyll*, which, in the presence of sunlight, enables living protoplasm to convert atmospheric carbon dioxide and water into carbohydrates, is the factor which led to the origin of plants; animals, on the other hand, must have had their carbohydrates elaborated for them.

As is well known, Haeckel gave the name PROTISTA to the group of primitive organisms which is supposed to be at the base of this dichotomy; its chief use, from a classificatory standpoint, was that it provided a name for those organisms which are not obviously plant or animal, but, at the same time, it introduced an additional difficulty, that of deciding whether a given organism was plant, animal, or protist.

Nowadays less attention is given to these matters than formerly. This is not because biologists do not believe that organisms are constantly changing; the opinion that is receiving more and more adherents is

that, until we know something of how these changes occur, the tracing of very extended descents is not as scientific as it was previously thought to be. We can arrange organisms in series, showing increased differentiation, and it is possible that development occurred along similar lines. When there is a fossil record the evidence for such a development is made stronger, but in organisms with no skeleton there is rarely any evidence to be gained from the rocks. Thus, in considering the data for evolutionary development in fungi and other lower organisms we have no assistance from the geological record.

Fungi are an enormous assemblage of organisms which are usually regarded as plants, but which differ from plants in general in that they do not possess chlorophyll; a few are green, but this is due to the presence of colouring matter of a different kind. Mushrooms, toadstools, mildews, rusts, smuts, and moulds are common names which will call to mind the organisms we are considering. Not possessing chlorophyll, they are unable to carry out the process of photosynthesis, the building up of their own carbohydrates, and in this they resemble animals.

To most naturalists the idea that organisms exist which are neither animals nor plants would seem startling. We are all so accustomed to consider these to be the only divisions of living organisms that anything out of the way is disregarded. Most fungi possess a definite cell-membrane, and obtain their food in solution by osmosis through this membrane, a method which is one of the main distinguishing marks of plants. Further, in attempting to trace the evolution of green plants, most modern botanists look to green algæ as their place of origin, whereas algologists apparently believe that green algæ themselves have evolved along parallel lines from green flagellates—*i.e.*, protozoa which had developed chlorophyll. Without attempting to discuss any nicety of phylogenetic

development it may be said, generally, that the usual belief is that green plants of all kinds had their origin in green flagellates.

If fungi are to be considered as plants they must, therefore, have been derived from green plants somewhere along this line. What evidence is there that fungi are colourless plants? It is well known that amongst flowering plants there are occasional forms which are colourless and which obtain their carbohydrates from dead or from living organic material. The first are known as *saprophytes*, the second as *parasites*; dodder (*Cuscuta*), broom-rape (*Orobanche*), bird's nest (*Monotropa*), and bird's nest orchid (*Neottia*) occur in our British flora. Though sometimes whole families are parasitic or saprophytic, the percentage, when the whole of the flowering plants are considered, is small.

A very commonly accepted view is that fungi have arisen from green plants in the same way as these colourless flowering plants have arisen from their green relatives—*i.e.*, by the adoption of a saprophytic or parasitic mode of life. The algæ are the chlorophyllous plants most like certain fungi in structure, and, in fact, the group which includes the simplest fungi is called PHYCOMYCETES, or algal-fungi, because of the idea that they were degenerate green algæ. It would take us too far to study these similarities in detail, but it may be said that, when examined closely, the resemblances are not more striking than would be expected in organisms of similar development occurring in much the same environment—*i.e.*, water or moist conditions. Moreover, on the view that Phycomycetes have arisen from green algæ by the loss of chlorophyll, and having regard to the resemblances, we should have to look to several different points for their origin; in other words, fungi must have arisen several times just as have colourless flowering plants. Such a polyphyletic origin, although feasible, is unlikely. One

of the difficulties on this view is the explanation of the origin of many unicellular fungi. These are not unlike the simplest algæ, but they show evolutionary tendencies amongst themselves so clearly that they are always regarded as having had a common origin with the filamentous forms. There are thus two ways of considering these simple forms: either they are primitive and have been derived from some colourless flagellate group, or they are reduced from filamentous forms which originally possessed chlorophyll. Upholders of the second view regard them as having become reduced by the adoption of a parasitic habit. It is common knowledge that many organisms become reduced when they adopt a parasitic or saprophytic mode of life. This is so, for example, with the vegetative organs of the colourless flowering plants previously mentioned. It is necessary, however, to consider what we mean by reduction, for it is often overlooked that sometimes it is really specialization. A colourless flowering plant could not exist unless it was able to make use of food already elaborated: it must have acquired the ability to live saprophytically or parasitically. The *Rafflesias* of Sumatra, with enormous flowers, the largest known in fact, have their vegetative organs reduced to cord-like structures, which permeate the roots and trunks of the woody hosts on which they are parasitic. Regarding these vegetative organs as stems, leaves, and roots, we are left amazed at the reduction which has occurred, but this so-called reduction has led to the perfecting of organs adapted to a parasitic mode of life which are without their equal apart from fungi. This gives us the clue for the proper interpretation of the *Phycomycetes*. If these began as green algæ and then, becoming parasitic or saprophytic, lost their chlorophyll, can we reasonably assume that their vegetative structure has been reduced until we are left with an extremely simple structure, and then explain the

evolution of myriads of different kinds of fungi by the success of the parasitic and saprophytic habit? The unlikelihood of the view is made more apparent from the fact that, if reduction by parasitism is assumed, we have also to attribute to it a loss of sexuality, for in the filamentous forms we have a well-marked male and female organ, whereas in the simplest forms fusion occurs between similar motile cells.

The groups of fungi other than *Phycomycetes* have been considered to have their origin either directly or indirectly from red algæ. The resemblances here are mostly in the more abstruse details of sexual reproduction, but, when analyzed, do not appear sufficient to serve as a basis for assuming relations. It is probable that these similarities would never have been regarded seriously had it not been for the belief that fungi *must* have been derived from green plants.

What, then, is the present opinion in these matters? There is, as one would expect, some divergence of view, but the one which is becoming more generally accepted is that fungi were originally derived from colourless flagellates related to the coloured forms which gave origin to algæ; that they have evolved by perfecting the parasitic and saprophytic habit; and that the principal groups of fungi are more closely related to each other than they are to any group of algæ.

We are thus led to the conclusion that fungi are not plants at all in the ordinarily accepted sense of the term. They are studied by students of botany and they are classified with plants in herbaria: this is because they are traditionally plants. Though they appear to have developed independently of plants, they are much more closely related to them than they are to any group of animals. As they reproduce by spores and not by seeds they are placed in the *Cryptogams* with ferns, mosses, liverworts, and algæ.

Although the structure of fungi is at least as varied and as interesting as that of any organisms, it is owing

to the consequences of their peculiar physiology that fungi are of general interest. Their activities are of many kinds—some beneficial to other organisms, some harmful. They vie with flowering plants in the number of species, and vastly excel them in the numbers of individuals. They vary in size from a single microscopic cell to bracket-fungi (*Polyporus*). Broadly speaking, they may be said to occur wherever there is organic life, and, if it were not for fungi and the very similar bacteria, life as we know it would be impossible. It is impracticable to deal with such a heterogeneous group here in detail, but a summary of some of the aspects of fungal existence may help to show the importance of these organisms in the scheme of nature.

CHAPTER II

STRUCTURE

As has been said, fungi reproduce by spores. Spores are the analogues of seeds, but, whereas seeds contain miniature plants, or embryos, which, on germination, provide the first root, stem, and leaves, spores contain nothing but more or less undifferentiated contents—protoplasm, nuclei, and sometimes reserve food material. Spores are usually microscopic, and though, as we shall see, they are occasionally motile, by far the greater number have no means of self-propulsion. The non-motile spores are usually spherical or elliptical, though sometimes very strange shapes may be assumed. They may be continuous or may be divided into segments by walls. The colour of the spores also shows a very wide range. However, given any species of fungus, no matter what its habitat or the conditions in which it has grown, its spores are found to be remarkably constant in size, shape, and colour.

When a spore is favourably situated it germinates usually by putting out a narrow tube, the germ-tube, from one or more places in its walls. Germination is not a strictly correct term for the process, for, as we have seen, the spore does not contain a germ; there is, however, no objection to its use if the difference between spore and seed is clearly kept in mind. In the majority of fungi the germ-tube elongates to form a thread-like *hypha*. Many hyphæ together constitute the *mycelium*, or "spawn," as it is called in the cultivated mushroom. The mature form is assumed later, and is essentially a spore-bearing structure. In

the larger fungi this sporophore is formed by the intermingling of hyphæ.

One of the most startling facts about fungi is the enormous number of spores that are produced. The common microscopic forms, such as the green moulds (*Penicillium*, *Aspergillus*), which occur on bread, jam, old boots, and other organic materials, produce myriads of spores, with the result that the air contains so many of them that it is necessary to take special precautions if contamination of foodstuffs is to be averted. Throughout the fungi there is this same prodigality. Buller has estimated the number of spores formed by the larger fungi, and arrives at figures far in excess of those for egg-production in the most prolific species of fish. A specimen of the common field mushroom (*Psalliota campestris*) with a cap 8 cms. in diameter, was found to produce 1,800,000,000 spores, whereas a giant puff-ball (*Lycoperdon Bovista*) contained as many as 7,000,000,000,000. In these numbers lies the explanation of the seemingly mysterious appearance of moulds or of that deadly trouble to the householder, dry-rot. When we imagine the millions of microscopic spores disseminated by air-currents, the difficulty is not so much in accounting for the occurrence of the fungus when conditions are favourable to it, as, for example, the lack of ventilation and the presence of moisture in dry-rot, but how, with such apparently universal distribution, any suitable substratum is not immediately colonised. Sterilization with a subsequent prevention of infection is possible only in special circumstances, and recourse otherwise has to be had either to treating a substance with an antiseptic, some disinfectant or preservative which has a deleterious effect on the fungi concerned, or so to arrange conditions that spores falling on substances which it is wished to preserve shall not find there the factors favouring their development.

As fungi do not possess chlorophyll, light is not necessary for their metabolism. It is not surprising, therefore, that many fungi develop quite normally in the dark, specimens found in caves or mines being indistinguishable from those living in the open. The cultivated mushroom, for example, is frequently grown in sheds, cellars, or railway arches, and the centre of the French industry is the caves in the environs of Paris left after the excavation of building-stone. Light, however, acts as a stimulus on the development of some fungi, which assume peculiar stag-horn-like shapes if light is absent. The fungus *Lentinus lepideus*, a toadstool which causes destruction of railway sleepers and wooden paving-blocks, forms no cap in the dark and directs itself towards a weak source of light; the cap is formed only in light of a certain intensity, and, after its initiation, the stipe is no longer heliotropic. Light also is effective in influencing the direction of spore discharge in many fungi. This is probably most marked in numerous species which grow on dung, and has been supposed to be an adaptation for the spore-producing organ to orientate itself in such a manner that the spores are shot to the greatest distance, with the additional suggestion that alighting on grass they would be eaten by herbivorous animals and, passing unchanged through their digestive tract, be effectively sown.

All fungi have a definite range of temperature over which they can grow. Other factors being constant, there is a minimum and maximum temperature, beyond which growth cannot occur, and an optimum temperature which is most suitable for growth. These temperatures vary considerably with different species. For example, some moulds are able to grow on cold store meat at a temperature of -6° C.; dry-rot often appears in cold store chambers, whereas its maximum temperature is about 34° C., consequently it does not grow in the tropics and, as the maximum temperature

is below that of blood-heat, the anxiety often felt about human illness caused by this fungus is unfounded. Most fungi will not grow at such low temperatures, although the spores retain their vitality. An interesting experiment by Becquerel showed the amazing vitality of the spores of some common moulds (*Mucor*, *Aspergillus*). These were slowly dried and placed in tubes from which the air was evacuated. The vacuum was maintained for over two years, during which time the tubes were subjected to the action of liquid air for three weeks and liquid hydrogen (the lowest temperature so far attained) for seventy-seven hours. Slowly brought up to ordinary temperatures, the spores readily germinated when they were sown on nutrient media. It is a common experience to find that spores and mycelium, after being dry for several months, or even years, will revive when placed under conditions suitable for growth. It is this ability of spores to withstand high temperatures that makes even boiling not a certain method of sterilization. In ordinary laboratory work sterilization is conducted either with steam under pressure, or, if this is impracticable for any reason, by boiling for about twenty minutes on three successive days; by the third day, as a rule, all the spores have germinated and the mycelium succumbs to the heat. It is not at all clear how spores are able to withstand extremes of temperature fatal to hyphæ, for usually they appear to have no special characteristics which can be regarded as adaptations for the purpose; many moulds have spores which appear to be nothing more than portions of mycelium separated off for purposes of dispersal.

This is all the more surprising because there are several ways in which fungi apparently do show adaptations for overcoming adverse conditions. Cells of the mycelium may become surrounded by a supplementary membrane, thus forming thick-walled bodies

called *chlamydospores*. Though, in some fungi, *chlamydospores* occur as normal structures when conditions are favourable for growth, in others they appear only when there is lack of moisture or of nutriment. A more obvious adaptation is met with here and there throughout the group where masses of compacted mycelium, sometimes with a specially thickened exterior, are able to remain in this condition for long periods, and then, when, mycologically speaking, matters become more suitable, resume growth and put forth fruit-bodies. *Sclerotia* are the best known of these dormant bodies. They are usually oval or spherical and, according to the fungus which forms them, vary in size from that of a small seed to that of a boy's football, the size corresponding roughly to that of the fruit-body. Many large *sclerotia* have long been known in the sterile condition, and it is only in the last few years that the fruit-bodies have been obtained. The first of the large *sclerotia* to be described was the *Tuber regium* of Rumphius (1750) from Amboyna, and though the attached toadstool was figured, there is still some doubt about the exact species. The view first held was that the fruit-body in these forms was parasitic on the *sclerotium*, but it is now realized that the two are genetically connected. Many large *sclerotia* are eaten by natives; several of these occur in Australia, the best known being *Polyporus Mylitta*, Blackfellows' Bread, and also in West Africa, where they are formed by species of *Lentinus*, very like the figure given by Rumphius. *Pachyma cocos* (*Poria*) and Tuckahoe (*Polyporus*) are well-known American forms whose perfect stages have recently been ascertained. All these are true *sclerotia*, being composed wholly of fungal mycelium. Similar but much smaller structures are formed by several common British fungi. Sometimes bodies resembling *sclerotia* occur, but differ in having earth and stones contained in the mass. The Italian

Tuberaster, or fungus lapidifer (*Polyporus*), known from classical times and mentioned occasionally in English literature, is such a structure. Here the fruit-body is easily obtained merely by watering the resting stage. As the fruit-body is esculent, the method of producing it has been practised through the ages. That a stone should give forth a mushroom greatly interested Pepys, who ardently desired to possess a specimen.

Sclerotia are not the only structures which we find composed of sterile compact mycelium. Mycelial cords or strands frequently occur, especially in the puff-ball group (*Gasteromycetes*). These strands are usually formed of hyphæ which show no differentiation, but occasionally there are different kinds of hyphæ in the strands, suggesting adaptations for withstanding strains without snapping and facilities for the easy conduction of food materials. On the whole, they are to be regarded as serving for the spread of the fungus in a manner similar to the way in which strawberry runners act rather than as resting bodies. The dry-rot fungus (*Merulius lacrymans*) possesses mycelial strands of a complex kind, ordinary hyphæ being intermingled with strengthening hyphæ and conducting hyphæ. When spores of the fungus fall on damp wood in a confined atmosphere they germinate and the hyphæ infect the wood. Some destroy the substance of the wood. Half the product of destruction is water; drops of this are exuded by the fungus, and, in addition to giving it its specific name, mislead the uninitiated into thinking that the trouble is not *dry-rot*. In addition to the hyphæ within the substance of the wood, other hyphæ become joined into silvery sheets much like fish-skin in appearance. The further spread of the fungus is generally brought about by the formation of the mycelial strands. These can pass along stone or metal, and even through the mortar of walls, though no nutriment can be de-

rived therefrom, and so eventually reach fresh wood-work; which they forthwith attack, spreading "the leprosy of a house" until it may become literally uninhabitable. The dry-rot fungus is practically confined to worked wood in buildings, though there is a special form of it occasionally found in woodlands.

Another highly destructive fungus, the toadstool *Armillaria mellea*, which attacks standing trees, also possesses differentiated mycelial strands. These, which pass through the soil from an infected tree, look like black leather boot-laces. Reaching a tree they force an entrance, and flattened anastomosing strands are formed under the bark. An interesting point about the rhizomorph of *Armillaria mellea* is that it is luminous when young. Further, freshly infected wood is luminous, and the majority of the accounts of "phosphorescent wood" in this country refer to this fungus. Luminosity is not of very common occurrence among fungi, and, so far as is known, is not of any biological significance where it does occur. Sometimes only the mycelium is luminous, as in *Armillaria mellea*, sometimes the whole fruit-body, as in the American Jack O'Lantern (*Clitocybe olearia*), which, incidentally, also occurs in Europe and North Africa. Several species of *Lentinus* are luminous and, as several of them are tropical, they have been used by natives for various purposes such as ornaments for women's hair. The light emitted is usually slightly bluish or greenish. It can be seen at a distance of several yards, and shadow photographs can be taken by its aid. Oxygen is necessary for its production, and light ceases to be emitted below freezing point. Certain species appear to differ in the individual possession of the property. *Panus stipticus* has a luminous sporophore in North America, but is non-luminous in Europe, whereas the common *Xylaria Hypoxylon* appears to vary, some investigators finding it luminous, others not. The rhizomorphs of *Armil-*

laris mellea enable the fungus to spread from tree to tree, the food for the advance being supplied by the tree or stump from which the infection starts. Mycelial advance and spore dispersal form the chief ways by which fungi spread.

It is a remarkable fact that when we consider what are usually regarded as special adaptations in fungi, we find not infrequently that the explanations we are able to suggest concerning the benefits derived from them leave us bewildered when we consider other fungi which seem to make no special provision. It has been mentioned that spores with no apparent organization against inclement conditions are able to withstand extremes of temperature and intensive drought, which without direct evidence we should regard as most unlikely. Although mycelium is usually not so hardy, it is only a matter of degree, and we have the same difficulty in explaining how an ordinary mycelium with thin walls is able to last for a considerable period. Everyone must have noticed how a toadstool will appear on a garden stump annually for many years. The mycelium of the fungus here is in the wood, and is consequently protected, but it is known that mycelium perennates in the soil in the same way. A fungus will occur year after year in the same spot and nowhere else in the neighbourhood. The best known example of a perennial mycelium is, however, that of "fairy-rings." Meadows, downs, and other grass-lands usually show darker rings of grass here and there. Often these rings have a bare patch in the middle in such a way that, when closely examined, they are seen to consist of three concentric circles, a middle bare zone surrounded by a narrow outer, and a broader inner, zone of darker grass. It is this bare zone which suggested to the poetically minded that it was worn during the midnight frolics of fairies, or in some other equally mythical way. It is a matter of simple

observation that, after heavy rain, water stands on the bare portion in the same way that it does on footpaths. Here, however, the soil is unable to absorb it, not because it is compacted together, but because the interstices are filled with fungal mycelium. The darker green portion of the ring shows much larger and more healthy looking plants than occur in the surrounding meadow, and they have the appearance of having been manured. This is, indeed, what has happened. When a fungus spore germinates it puts out a hypha which elongates, branches, and grows in all directions at approximately the same rate, forming a circular growth. The fungus lives saprophytically at the expense of organic substances in the soil, and in doing so liberates materials which act as chemical manures for the grasses and meadow plants. These are stimulated to increased growth, and consequently make greater demands on the soil moisture than formerly. Meanwhile, the fungus continuously advances and increases greatly in amount, causing the soil to become impervious to water. The luxuriantly growing plants are thus unable to obtain the moisture they need; there is a physiological drought, and the plants die and leave a bare zone. The mycelium continues to advance, but as it progresses it dies off behind. The bare patch is then recolonized by grasses and other plants, and these, in their turn, are manured by the altered remains of fungal mycelium and fruit-bodies. It is this stimulation which accounts for the luxuriance of the plants in the inner zone.

The rate at which the ring increases in diameter over a number of years gives us an average annual rate of advance. By dividing this into the diameter of the ring we obtain a rough estimate of its age. This is found to be of quite unexpected dimensions, often reaching a century, and occasionally as much as four centuries. When the vicissitudes a mycelium must undergo during such a period are considered,

one is amazed at the tenacity of life which it displays.

Another aspect of the consequences of a perennial mycelium arises from a consideration of fairy-rings. The rate of progress is dependent upon climatic and soil conditions, but, whatever these be, there is almost always a crop of fruit-bodies. The commonest ring-forming fungus is the fairy-ring champignon (*Marasmius oreades*), but very many toadstools form circular growths. As we have seen, one of the characteristics of these fungi is the enormous numbers of spores they produce. When a toadstool is examined it is found to consist essentially of a spore-bearing surface usually arranged on gills or tubes on the underpart of a cap which is borne on a stalk. The spore-bearing surface is mainly composed of serried ranks of clavate organs with normally four projecting teeth on which the spores arise. Without entering into details it may be said that the whole forms a highly co-ordinated structure to ensure the efficient dispersal of the spores which are shot off from the gills. Millions of spores are formed, and the vast majority are effectively distributed. What is their fate? At first thought it would appear that all that remains to be said is that widely scattered by air-currents they fall on suitable ground, germinate, and bring forth their fruit-bodies in due season. But how many spores have such a future? How many of the seven million millions of spores of a giant puff-ball will in their turn produce a puff-ball? The answer is to be found in Darwin's discussion of the prodigality of seed-production in orchids. Other things being equal only one of these spores on an average will thrive effectively, for otherwise there would be an increase of puff-balls to such an extent that there would be no room left in the world for any other organisms. Thus, we must assume an enormous wastage of spores. A consideration of fairy-rings only adds to the difficulty. The giant puff-

ball itself often forms enormous rings, and, consequently, if one spore is sufficient for the production of a ring, one spore alone is effective during the age of that ring, whether this be a few years or centuries.

It is not only in fairy-rings that we are brought startlingly face to face with this enormous spore-wastage. Bracket-fungi, which occur on trees, often have a life of several years; as many as eighty annual layers have been recorded for *Fomes igniarius*. Here the fungus liberates spores continuously day and night for six months of the year, and presumably all of these result only in another sporophore establishing itself eventually and devoting itself to the mass-production of spores.

Correlated with the spore-wastage considered above, we have to realize that with many microscopic fungi no substratum which would allow of their growth appears free from them. The air contains myriads of spores of all kinds which settle on everything, and where conditions are favourable to growth infection occurs. Even with the most successful moulds, however, we have to envisage an enormous wastage. Whether or not this reaches the same percentage that it does in toadstools and their allies we have at present no means of estimating. All that we can say is that presumably moulds do not become more prevalent with the years.

CHAPTER III

FUNGI AND MAN

THERE are many aspects of mycology, the study of fungi. The one which appears to give most promise of immediate interest is that which is due to their essential physiology. Not being able to form their own organic foodstuffs, they are in very close relation with other organisms. Abandoning structure and classification, excepting in so far as these are necessary for the understanding of the points considered, the main line of treatment here followed will deal with the relation fungi bear to man and his activities, to insects, and to plants.

Man probably first regarded fungi as a possible source of food. From the earliest times we find records of this interest, and one of the earliest attempts to classify fungi was that of Dioscorides, who divided them into edible and poisonous forms. There are numerous references in classical writings to the ways of distinguishing between these two groups, and every year newspapers and magazines have articles giving sure and certain signs of judging which species are worthy of the pot. All these rules are worthless, with the possible exception of the one often repeated of old, that fungi which grow near serpent's holes are poisonous.

There appears to be only one fungus concerning which there is no doubt that it causes the death of healthy people, though some of its allies and other suspicious species are equally to be avoided. This toadstool is *Amanita phalloides*, and all the commonly accepted rule-of-thumb methods break

down with it; it peels and it does not turn silver black! Records taken over the last half-century or so show that ninety per cent. of deaths caused by fungi are due to this fungus. Moreover, the death is an agonizing and lingering one; a French account ambiguously states that the patient, if he is lucky, dies on the third day. The number of fungi which are really poisonous is exceedingly small, probably not five per cent. of all the toadstools, though there are other points than mere edibility which enter into the problem. To be told that a fungus tastes like saddle-flaps or smells like bugs is sufficient to stifle appetite. If one wishes to indulge in mycophagical experiments nothing beyond a little intestinal discomfort would result if about a dozen species are excepted, and it is just as easy to learn the same number of well-known edible species. Most people are satisfied with about twenty; these incidentally are as markedly distinct and distinguishable as are flowering plants. There are several of them which are at least equal in flavour to the cultivated mushroom, and they are commonly sold in Continental markets though not now in this country.

Thus, though there is no simple way of deciding whether a given fungus is edible or not, comparative safety may be ensured if a few species well known to be poisonous are avoided, and absolute safety and appetizing dishes if one restricts oneself to a few species which have been of good repute through the ages. Here, as elsewhere, however, personal idiosyncrasy has to be taken into account.

Truffles, which always have been highly prized, are subterranean fungi, and, consequently, difficult to find. As they have a characteristic odour, dogs or pigs are trained to hunt for them, the digging being done by the owner of the animal. Truffle-hunting was carried out on the South Downs until comparatively recently, but now appears to have died out.

Many attempts have been made in Europe to cultivate edible fungi, but so far successfully only with the common field mushroom (*Psalliota campestris*). The cultivation of this species apparently began in France, the first account of it being that of Tournefort in 1707. Mycelium ("virgin-spawn") is gathered from pastures, under hay-ricks, and so on, by expert gatherers who are able to distinguish it. This is used for inoculating "bricks," which are usually made from a wet mixture of stable-manure, cow-manure, and a small quantity of loam. The virgin-spawn is inserted while the bricks are still moist, and precautions are taken to ensure that when dry the brick will be thoroughly permeated with the mycelium. Mushroom beds are made up of "compost," which is stable-manure allowed to ferment for about three weeks. When the beds have become cool enough they are "spawned," and after the mycelium is "running" satisfactorily the beds are cased with an inch or so of fairly rich loam. Mushrooms are produced after from six to eight weeks and bear for from two to four months. Attempts have been made to obtain spawn from the spores of the mushroom, but the only successful commercial method has been kept as a trade secret by the French firm which perfected it. There is, however, a pure culture method which has been worked out by the U.S.A. Department of Agriculture. It has been found that virgin-spawn can be replaced by cultivating small pieces of the internal tissue of young mushrooms on manure and half-decayed leaves under conditions that prevent contamination. The chief advantage of the spore method and the tissue-culture method is that when a mushroom with any desired qualities is obtained its propagation is assured.

The only other fungus cultivated on a commercial scale is the Japanese Shiitake (*Cortinellus Shiitake*). The method is several centuries old. The fungus

occurs naturally on chestnut and on oak, and poles of these are cut and allowed to weather. Small holes are then bored in them and powdered, infected wood is inserted. The fruit-bodies begin to appear after about two years. Though fungi have been eaten by man for thousands of years, their food value is small. They resemble green vegetables in the amount of water they contain, and much of their substance is not in a digestible condition. Their chief value is as appetizers in giving variety and flavour to more nutritious but less interesting foods.

The direct use of the larger fungi by man is, however, not so interesting as the indirect use he makes of the smaller forms. To explain this it is necessary to consider one or two general points. Many organic substances occur which are not readily assimilated by fungi unless some change is brought about in them; in other words, in an unaltered form they cannot be digested. Fungi, however, like all other organisms, possess substances called enzymes or ferments, which are able to bring about these changes. We know little about the exact nature of these enzymes, but they appear to be protein or nucleo-colloids in a dispersed form. They are not used up during the reaction they bring about, and resemble catalytic agents. Some enzymes are specific in their behaviour and are able to act only on a single substance, whereas others are more catholic in their activities, being able to bring about changes in a series of related substances. The number of enzymes which a fungus possesses often seems to bear no strict relation to the life that the fungus normally leads, as many as fourteen having been recognized in some species. When we are considering the action of a fungus on any substance we have to envisage the gradual solution of this by means of enzymes which are secreted by the hyphæ, and the absorption of the resulting compound through the cell-wall. Enzymes also enter into the more inti-

mate life processes of fungi in a manner which demands a deeper treatment than can be given here. The point to realize is that, so far as we know, all the essential chemical changes in organisms are brought about by enzymes, which are formed by the organism.

Our first knowledge of enzyme action or fermentation goes back as far as man's history. The ancients well knew that if fruit juices were left exposed to the air the liquid became cloudy and gave off bubbles of gas, which made the liquid appear as if it were slowly boiling, and that the liquid gradually became alcoholic. The making of wine in this way continued down to recent times, with no accurate knowledge of the essentials of the process. Man, in a similar empirical way, learned to prepare cider and perry from apples and pears, mead from honey, and so on. The art of distillation dates back at least to 2000 B.C., so far as it relates to beverages. All these fermentative processes are dependent upon the action of minute fungi known as yeasts. There are a large number of yeasts, and they are to be found on the skins of fruits, in the soil, and in the air. They are classified into families, genera, and species in the same way as are larger fungi. Most of them in their normal form consist of a single ellipsoidal cell which, when it is placed in suitable conditions, produces a nipple-like outgrowth which increases in size until it is similar to the mother cell and then is separated off. This method of "budding" is almost confined to yeasts. When yeast cells are grown in a solution of sugar they break up the sugar into alcohol and carbon-dioxide, using some of the energy which is thus released for growth.

In the fermentation processes, so far mentioned, the presence of the yeast is more or less haphazard, but, in the preparation of the better known bread and beer, yeast is definitely added. The Old Testament

contains references to leavened and unleavened bread—that is, bread which has been allowed to “rise” or not. Doubtless this method was the result of finding that dough which was left for a time made better bread. A portion of the sour dough was later kept for adding to the next bake, a method which is used to the present day. In countries where it is obtainable, however, distillers’ yeast is preferred. This acts on the sugar, breaking it down to alcohol and carbon-dioxide; the gas distends the dough, making it porous with a resultant light bread.

Beer is prepared from barley which is allowed to germinate and then dried. This malt is then steeped in water, during which process the starch is converted into sugars. The extract is separated and boiled with hops. The liquid (wort) is rapidly cooled and yeast is added; this acts on the sugar with the production of alcohol. Modern brewing is a highly scientific process. The yeasts used are chosen, cultivated strains which are kept pure and retained for the production of special brands. We owe much of our knowledge of the biological processes concerned to the pioneer work of Pasteur, undertaken as a direct result of the disasters his country endured after the Franco-Prussian war. Most nations have their primitive alcoholic beverages, and in all of these, whether they are fermented milks (kephir, koumiss, leben), fruits and seeds (saké, arrak), or plant juices (pulque), yeasts are concerned, either alone or in combination with bacteria or moulds. Sometimes the different organisms carry out the separate parts of the process independently, whereas in some yeast-bacterium associations the relation is so intimate that it is frequently regarded as symbiotic.

The general tendency now is to attempt to carry out fermentative processes under properly controlled conditions. Within recent years the ripening of cheeses, which is due to species of the genus *Penicillium*,

has been accomplished by definite inoculation instead of relying on chance infection. There are many other ways in which the fermentative activities of fungi are being harnessed for man's use. The production of certain organic acids (fumaric, butyric, citric) is commercially possible by fungal action. Industrial alcohol is now extensively prepared by acting on starchy substances with a mould (*Mucor* spp.) to convert the starch into sugar and then fermenting the product with yeast. Commercial diastase, which is used in various textile industries, and also in medicine, is usually prepared by growing *Aspergillus Oryzae* on bran and extracting the enzyme with water.

The above outline suggests that with increasing knowledge we shall be able to carry out what are now regarded as intricate chemical operations by the proper use of fungi and bacteria. A further intimate relation between man and fungi is that which results in disease. The majority of organisms are liable to a condition where their normal functions are interfered with in some way. Much of this disease is caused by parasitic organisms; even fungi may be parasitized by other fungi! Fungi, from their physiological necessities, are either saprophytes or parasites, and man is not immune from their attacks, though human fungal diseases are very few compared with the number due to bacteria. The best known fungal diseases of man are "ringworms" and various skin infections, common in the tropics, but rare elsewhere. Ringworm is due to the radiating growth of the mycelium of *Trichophyton* and allied fungi, some affecting the hair, some the skin. They are simple in structure, consisting merely of hyphae, which sooner or later bear spores. In some tropical skin diseases due to these fungi multiple infection and subsequent radial growth results in the production of extraordinary conventional designs. Various other animals, such as the horse, the dog, and the cat are affected

by ringworm, and it is not at all uncommon for the infection to be passed from them to children.

"Thrush," an affection of the mucous membrane of the throat, caused by a yeast-like fungus growing in the milk of dirty feeding-bottles, is now less frequent in infants than it was formerly. Similar yeast-like fungi are reputed to cause bronchial troubles. It is probable that the presence of yeasts and similar fungi in the intestinal tract cause disturbance; "sprue" is now thought to be due to these. "Lumpy jaw," which is mainly an infection of cattle, is, like ringworm, not infrequently transmitted to man. Ostlers are said to be the chief sufferers, becoming infected mainly through their habit of sucking straws.

Diseases of the foot, causing it to become ulcerated, deformed, and useless, occur amongst natives in semi-tropical regions. There are several forms, the best known being "Madura foot"; all appear to be due to fungal infection. Our knowledge of medical mycology is yet in its infancy, but increasing attention is now being paid to it. Time and again there are indications that the fungi responsible for many diseases are able to live saprophytically, growing on plant remains or other organic debris.

CHAPTER IV

FUNGI AND PLANTS: PLANT PATHOLOGY

MAN is dependent for his existence on the plants of the field. He and his herds and his flocks, no matter what their inter-relations, are doomed without his crops. When crops fail, whether of wild or of cultivated food-plants, then there is famine and pestilence.

The old English words "blight" and "blasting," which were commonly used to signify damage in crops, sound of evil and forbidding import even to modern town-dwellers who are now but little affected by these things, for before the days of rapid transport they might mean famine and death. It is easy to understand how our forefathers, when they saw their crops suddenly swept through, believed that the blight or mildew was a symbol of divine wrath, and there are many references in the Bible to this. When scientific explanations began to be sought all the "elements" seem to have been held responsible, as well as the various "vapours" and "exudations" which abounded in early scientific jargon. There are occasional hints that fungi were sometimes implicated. Thus we find that Robert Hooke, when he was examining all the objects he could with his newly invented compound microscope, found that the rust on the under side of the leaves of damask rose was a definitely organized structure, which he compared with a minute mushroom; he gives a recognizable figure of it in his *Micrographia* (1665). Many other observations followed, but a not uncommon view was that the structures seen were not entities, but were external manifestations of the diseased condition. In other words, though definite

microscopic organisms occurred on blighted plants, these were formed by the plant itself.

A change of view took place during the investigations on potato blight. This disease appeared in Europe about 1840, and more or less simultaneously in America. It soon reached an epidemic form and swept through Europe, reaching Ireland and causing the terrible potato famine of 1845 and 1846 which had such important results on the political history of the British Isles. Four separate commissions were appointed by different European countries for its investigation. It began to be realized that the disease was caused by a fungus, a Phycomycete now known as *Phytophthora infestans*. One of the leading investigators of the disease was the Rev. M. J. Berkeley, who, by his clear statement that the fungus was the cause of the diseased condition and not a result of it, is usually regarded as the father of plant pathology.

In the last paragraph the term disease has been used: blights, blastings, mildews, rusts, smuts, and so on are popular names for what are really diseases of plants, though some of them are also used by mycologists for the fungi which are responsible for the disease. The diseases of plants are in the main due to fungi or insects, though a number are caused by bacteria, or by filter passing organisms—leaving out of account those unhealthy conditions due to bad cultivation. It would be little exaggeration to say that all trees, herbs, and shrubs have their parasites, though the majority of these do little apparent harm to the plants. Severe damage, however, is not likely to be noticed except in trees, and it is not infrequent to see these with parasitic bracket fungi on their boles, hollowed by them, or even killed. On the other hand, anything affecting the well-being of cultivated plants is regularly noticed. Apart from this, however, cultivated plants are more likely to become infected by parasitic fungi than are those growing wild. Man has his own ideas about the

qualities he wants in his crops and, by selecting and breeding, has produced plants differing greatly from the natural original stock. Sometimes such plants are not so hardy as their ancestors and, moreover, the conditions under which they are cultivated differ greatly from those of the wild state. Manurial feeding, for instance, has its effects, as we see from the excessive rusting where rich nitrogenous manures are used.

When once disease has started, infection spreads rapidly, because a large number of the spores formed must find a victim, whereas in natural conditions, where individuals of the same species are widely separated, there is not the same chance of the spores reaching them. A further point is that crops are frequently alien to a country. So far as their native habitat is concerned they may be regarded as being in a state of equilibrium with their environment, which includes potential parasites. When plants are introduced into a new country they are often subjected to the attacks of a fresh series of parasites, often with disastrous results. The reverse is seen when parasitic fungi are introduced into a new country. The fungus appears to receive an impetus in a manner similar to the often quoted rapid spread of the rabbit when introduced into Australia. For example, a fungus is believed to have been accidentally introduced into America from Japan on ornamental chestnuts about 1904. It attacked the sweet chestnuts in and about New York and rapidly spread, so that the whole of the Eastern States is dotted with dead stumps and the cultivation of the tree is no longer possible. Several governments have passed strict quarantine laws in the endeavour to obviate the chance introduction of pests into a country at present free from them. Phytopathologists are not in agreement about the efficacy of the method, even though it be carried to the length that it is in the U.S.A., where all plants which are not horticultural novelties are refused admittance.

The ravages of the chestnut-tree blight, which is computed to have caused damage to the extent of something like £6,000,000 within seven years of its introduction into the U.S.A., is one of the striking examples of the effects of fungal disease. A better known one is the coffee-leaf rust which wiped out the growing of coffee in Ceylon, a flourishing industry in 1870. The industry was in a hopeless condition within ten years, and the country was saved from ruin only by the fortunate introduction of tea planting.

The effects of all fungal diseases are not so dramatic or so disastrous as the potato blight and the coffee-leaf disease, but they cause a steady and a worldwide loss, which, if it could be estimated with anything like accuracy, would reach incredible figures. The losses due to the downy mildew of the vine alone have been calculated as £500,000,000 annually. A U.S.A. estimate of the losses in their main crop in 1919 was that there was a range from 2 per cent. to 50 per cent.—losses of 190 millions of bushels of wheat, 200 million bushels of maize, and 86 million bushels of potatoes. It is the gradual realization of the extent of these losses which has led to the building up of phytopathological services in all civilized countries, whose work may be best described as being similar in principle to that of medical services, though in few countries is it yet so highly organized. An instructive way of looking at the relation between what is called the host plant and its fungal parasite is to regard it as a struggle between the two. Under certain conditions the host is able to withstand the attack of the parasite, but it will become parasitized if it loses tone in any way. Environmental conditions may reduce the resistance of the host or increase the strength of the parasite.

It is common knowledge to those interested in gardening that some varieties are more susceptible to attack than others; some varieties of rose always remain free from mildew, although others are infected.

Varieties of crop plants also vary greatly in resistance to a given disease. In searching for means of combating diseases much attention is now paid to the production of races of plants which will resist a given disease. There are various degrees in the parasite-host relation, ranging from immunity to death of the host, and many researches are in progress which aim at solving the factors which decide the nature of a given attack. For our purpose we may speak of a host plant, which becomes obviously diseased, as a susceptible plant and one which shows no apparent lesions as an immune one. Sometimes a plant is merely disease-escaping. Black rust (*Puccinia graminis*) does little harm in England, because the wheat has got so far ahead with its growth when the fungal attack occurs. Again, if the worldwide distribution of crops is mapped out and also that of their possible parasites, it is sometimes found that the area of the first overlaps that of the second. Thus, onion smut (*Urocystis*) is absent from large areas of North America where the onion is grown, because the crop is sown when the temperature of the soil is above that at which the fungal spores germinate.

Though the obtaining of immune varieties solves the problem of disease-prevention the plants must also be desirable in other ways. Most of the immune varieties, which have so far been produced, have been obtained by selecting individual plants which are free from the disease, and breeding them from seed or by vegetative means. Thus, wilt-resistant cotton has been got by seed selection. Another method which is of more scientific interest is the application of Mendelian principles. This was first made use of by Biffen working on brown rust (*Puccinia bromina*) in wheat. Immune varieties were known, but they were of poor quality. By hybridization experiments it was found that immunity to the disease was a recessive Mendelian character, which was overlaid by

the dominant susceptibility in the first generation, but appeared in its pure form again in the second generation. The results of a series of similar experiments showed which of the most desired characters of wheat were dominant and which recessive, and so the data were obtained for the building up of such varieties as Yeoman and Little Joss, which are now extensively grown in the British Isles.

These methods of circumventing disease are not yet of general application. More usual is the attempt to use sprays or dust, either as prophylactic measures or for controlling a disease when it has appeared. There are many fungicides, the best known of which are copper and sulphur, though arsenic and mercury are coming more into use: sulphur is the only one used in an uncombined state. The principle of the treatment is to cover the parts of the plant subject to attack with a film of the fungicide; the spores of the fungus are unable to germinate in this, and if mycelium is already present it is killed. The best known fungicide is Bordeaux mixture, composed of copper sulphate and milk of lime, first used for spraying wayside grapes to prevent the depredations of passers-by, and observed to be efficacious also against the much more troublesome grape mildew.

In the scientific study of plant diseases it is necessary to study the structure and physiology of the host plant as well as that of the parasite; the host-parasite complex has also its peculiar physiology. Where diseases are seed-borne they can be prevented by steeping the seeds in some chemical solution or by treating the seed with dusts. It is also becoming increasingly realized that general sanitation plays a large part in preventing the spread of the disease; this may be regarded as an attempt to grow a plant under the most healthy conditions, and the removal and burning of all plant litter which may serve as a source of infection, either by allowing the mycelium and

spores of disease-producing fungi to hibernate or by enabling these to have an intermediate situation which they may colonize and where they may live saprophytically, later to attack the developing plants.

One of the interesting points brought out by a study of the life-histories of disease-producing fungi is that many rusts carry out their life-cycle on two different host plants. This *heteraecism*, as it is called, was long suspected in wheat rust, farmers in many countries believing that the prevalence of the disease was influenced by the presence of barberry. About sixty years ago de Bary proved that they were right in their contention. So far as we know, the phenomenon is confined to rusts and to species of the Discomycete *Sclerotinia*.

Rust fungi are remarkable in the number of spore forms they may possess. Black rust of wheat (*Puccinia graminis*) first appears as rusty pustules on the leaf-blades and these gradually become black. The first colour is due to numerous orange-coloured spores which act as summer spores, being able to carry infection from plant to plant. The change in colour is on account of the replacement of the uredospores by cells with dark thick walls. These, the *teleutospores*, are resting spores or winter spores. They are unable to infect other wheat plants. After a period of rest they germinate, giving rise, not to an ordinary germ-tube, but to a structure with three cross walls, each segment producing a small rounded colourless spore. This peculiar structure is very similar to the basidium of the Jew's Ear (*Hirneola*) and its allies, and, consequently, rust fungi are classified as Basidiomycetes. The jump from wheat to barberry occurs at this stage, the basidiospore being able to infect this plant though not wheat. Two other spore forms occur on the barberry, one contained in a flask-shaped fruit-body, its function being still in question; the other in "cluster-

cups," being able to infect wheat but not able to spread infection in barberry.

Thus we have a well-defined alternation of hosts. The removal of the alternate host is an obvious way of keeping the disease in check, but there is a complication owing to the over-wintering of uredospores. However, in the northern part of the wheat belt in America the disease is controlled to some extent by the eradication of barberry. The white pine blister rust (*Peridermium*), which was introduced into America on nursery stock, is checked by the removal of *Ribes* species, on which the alternate stages of the fungus occur. The boll disease of cotton is caused by yeast-like fungi which are transmitted by plant-feeding bugs. In the West Indies the bugs live on malvaceous trees in the absence of the cotton crop, and these are removed as a means of control.

Many saprophytic fungi become parasitic under certain conditions, either those which are detrimental to the general health of the plant or are especially suitable to the fungus. Such, for example, is the common grey mould (*Botrytis*). The majority of diseases are, however, due to fungi which are wholly parasitic as far as we know; for with increasing knowledge the generalizations of a previous generation are found often not to have the wide application attributed to them. Many parasites are able to attack a whole range of plants, sharing this character with the facultative parasites and facultative saprophytes—that is, fungi generally saprophytic which may become parasitic and *vice versa*. The majority of parasitic fungi, however, are definitely limited to one host plant. This specialized parasitism occurs in all the main groups of fungi. It is also well known that many of the parasitic species of fungi consist of a number of strains, races or pure lines, morphologically indistinguishable, but separable on a physiological basis. Thus the black rust of wheat, as it occurs in North

America, has been segregated into about forty strains, which are distinguished by their reaction to pure line strains of wheat.

Most parasitic fungi are restricted more or less to certain organs of the host. Thus we can speak of leaf parasites, root parasites, and so on. Further, different groups of fungi cause characteristic diseases, and powdery mildew, downy mildew, rust, and smut can be distinguished at sight. The lesions and symptoms produced in the host plant or the malformation caused by the reaction of the host may be classified as wilts, die-backs, witches' brooms, blight, cankers, etc. A large number of fungal parasites are so characteristic in their action on a host plant that even if the disease is unknown a shrewd guess can be made as to their generic position. When a disease is known its diagnosis at sight is as certain as the ordinary clinical diagnosis of the general practitioner.

Though the classification and biology of parasitic fungi are of absorbing interest and of enormous importance to the plant pathologist, his main interest lies in the prevention of disease and a resultant increase in the world's food supplies.

CHAPTER V

FUNGI AND PLANTS: "SYMBIOSIS"

ANOTHER aspect of the relation between fungi and plants is that usually called symbiosis, where two organisms live constantly together. It is generally assumed that the association, because of its consistency, must be for the mutual benefit of the constituents.

I. MYCORRHIZA

A well-known association is that between flowering plant and fungus. As this is mainly concerned with roots the term mycorrhiza (fungus-root), which was applied to it about fifty years ago, is retained, though fungal hyphæ are not restricted to the roots; the term is, moreover, extended to similar associations between fungus and moss and liverwort, where there are no true roots. Much work has been accomplished on mycorrhiza during the last few years, and it is probable that before long we shall reach an explanation of many puzzling phenomena. The relation between flowering plant and fungus is not always the same and it is only cloaking our ignorance to label it "symbiosis," and then assume that there is equal give and take with a resultant mutual benefit.

The roots of the majority of flowering plants have fungal hyphæ associated with them sometime or other. Often this association is constant, but it is by no means invariably so. The hyphæ sometimes occur mainly on the outside of a root, enveloping it like the finger of a glove, at other times they occur principally within the cells of the root. The first

type is known as *ectotrophic*, the second as *endotrophic*. The two types are not wholly distinct, but are sufficiently so for the terms to be useful.

Ectotrophic mycorrhizas are best seen in forest trees. In the majority of trees many of the ultimate rootlets, which occur in the upper layers of the soil, are swollen and branched in a coral-like manner, sometimes being brightly coloured; they do not possess root-hairs. A section of such rootlets shows the rootlet itself as a core surrounded by a sheath of compact mycelium. Some hyphæ occasionally pass between the cells of the piliferous layer and enter the cortical cells of the root, but the majority of the hyphæ are external. The presence of the fungus and its development depends upon external conditions to a great extent. It is thought that the tree benefits by the passage to the roots of nutriment obtained by the fungus from the humus; it is difficult to suggest what benefit the fungus obtains. So far as has been experimentally proved, the fungi concerned are all of the toadstool group.

It is well known to those interested in field work that certain fungi are usually found in the neighbourhood of certain trees. Thus, *Boletus elegans* and *B. viscidus* occur under larch, *Amanita muscaria* and *Lactarius turpis* under birch, *Russula fellea* under beech, and so on. The mycelium of these can be traced to the coralloid rootlets, and, during recent years, Melin has experimentally achieved the formation of such rootlets by germinating seeds in a substratum in which the fungal mycelium was growing. Apparently more than one species of fungus can enter into association with an individual tree. Moreover, it seems probable that an association once established lasts for many years, for the fruit-bodies of the fungus may be seen growing in a ring about the tree and presumably keep pace with the gradually extending root system. The ectotrophic type of my-

corrhiza is best known in orchids and heaths. Sections of the roots of these plants usually show balls of mycelium in the cortical cells. In orchids some or all of the cortical cells may be infected. The mycelium remains fresh-looking for a time, but later begins to lose its outline and becomes, finally, a glary amorphous mass. At the same time changes occur in the nucleus of the orchid cell, which show that the clumping is due definitely to the reaction of the orchid. These facts have long been known, but a little over twenty years ago it was found that the mycorrhizal fungus played a peculiar part in the life-history of the orchid.

The seeds of orchids are very small and have little if any reserve food material. Further, their embryo is not differentiated into root, stem, and leaves, as is usual in flowering plants. It is not possible to germinate them by ordinary means, but it has been found that with special precautions they will germinate if supplied with sugar. The ordinary horticultural practice is to sow the seeds on the soil in which the parent plant is growing, or has grown. Frequently a good percentage germination is obtained in this way, and if the young seedlings are examined they are found to have some of their cells penetrated by the fungus. Bernard recognized the resemblance of this fungus to that of the root and established that if the fungus is extracted from the orchid plant and grown on a culture medium and the seeds then sown on it the majority of them germinate. The fungus enters the cells of the lower part of the seed, but does not penetrate into the growing point of the stem when this is laid down, nor, generally, into the young root when first formed. All infection apparently takes place from the soil. So far as is known, all the fungi found in orchid roots which are able to induce germination are of the same general type. The fungus is a mould very much like *Rhizoctonia*, long known as a parasite of potatoes and other plants. There are several

different types of the fungus, some of which may be species; others, showing less morphological differences, are probably only strains or races. These are all to some extent specialized to particular orchids. Thus, the fungus from *Odontoglossum* will not stimulate the seeds of *Cattleya* or *Cypripedium*, and *vice versa*.

Thus we have a number of closely allied fungi which are specialized to different orchids, and these, found constantly in their roots, are necessary for the normal germination of the seeds. It is probable that as the seeds which are produced in enormous numbers are almost entirely lacking in food reserve, and as their germination can be brought about artificially by supplying them with sugars, the fungus acts by producing these in the substratum or transports them into the seeds. That the mature plant also receives benefit would appear from the fact that in a series of plants those with a low chlorophyll content have a greater amount of fungal hyphæ in their roots than have those with a high content; other things being equal there is most fungus in the colourless saprophytic orchids such as *Neottia*. On the other hand, it is difficult to understand what real benefit the fungus obtains. For the most part it is finally absorbed in the root, and the advantages of dispersal appear to be slight.

The facts seem to point to the fungus originally having been parasitic and the infection later turned to the advantage of the flowering plant, which keeps it restricted in its distribution in the tissues and then kills it. That this is probable appears from what we know of a peculiar relation between a Japanese saprophytic orchid, *Gastrodia elata*, and the toadstool *Armillaria mellea*. The resting stage of the orchid is a potato-like tuber. When it grows it puts out an offset, and each year the new tuber is progressively smaller until eventually these are too small to carry on. When, however, the tuber is infected by the

rhizomorphs (*cf.* p. 19) of the fungus it puts out an off-set which grows into a flowering shoot. Now *Armillaria mellea* is one of the most destructive parasites known. When its rhizomorph reaches the tuber it puts out haustoria similar to those formed by the dodder (*Cuscuta*), and the mycelium of the strand passes into the cells of the tuber and forms tangled skeins similar to those of the endotrophic fungus of orchid roots.

Without entering into detail it may be said that there is a well-defined balance between tuber and fungus. When a rhizomorph encounters a potato tuber it rapidly converts it to a putrescent mass: on the other hand, when it meets with the similar *Gastrodia* tuber it sets up an association with it. From the fact that an infected orchid tuber leads to the complete development of the plant, it seems that the rhizomorph is converted from an organ serving for the spread of the fungus to a channel passing nutrient materials from tree stumps to the orchid which has no other source of food supply. Details of the seed germination of *Gastrodia* are still lacking, but what is known of the general biology of the plant gives us a clue to the interpretation of the peculiar relation which exists between many flowering plants and fungi.

A type of mycorrhiza very similar to that of orchids occurs in heaths (*Ericaceæ*). Most of these have an endotrophic fungus in their roots which is clearly seen tangled up in the cortical cells; a dissolution of the fungus also occurs. Here, again, the seeds are difficult to germinate, and it has been found that in common ling or heather (*Calluna vulgaris*) the seed is stimulated to germination by the fungus extracted from the plant. The fungus here is a species of *Phoma*, one of the Fungi Imperfecti, and, so far as is known, species of this genus are present in all *Ericaceæ*. A difference from the orchid type is that the fungus, though most obvious in the roots, is

present in an attenuated form throughout the plant-stem, leaves, and fruit capsule. It is probably from the fruit capsule that the seed coat becomes infected, and it was thence it was first obtained for germinating seeds. It has been stated that the fungus is able to fix atmospheric nitrogen, and thus benefit the plant which, owing to its usual habitat on poor soils, has difficulty in obtaining its necessary salts, but the proof of this is very difficult and the evidence for it is not at present satisfactory. Results on chemical stimulation have not yet been published, but it is probable that here, also, carbohydrates are contributed by the fungus. The benefit which the fungus gains from the association is again problematical. It may be that occasionally the balance between the component organisms is weighed down in its favour and it overcomes the resistance of the flowering plant, killing it and fruiting on its surface, but this is doubtless a rare occurrence and hardly seems an equitable recompense for its customary quota of service to its insistent partner.

Gentianaceæ and Burmanniaceæ are other families which have a general mycorrhizal condition similar to that of Orchidaceæ and Ericaceæ. It is an interesting coincidence, if nothing more, that these four families have small seeds with little or no reserve food material, and that it is in them that we find flowering plant saprophytes. It may be that flowering plant saprophytes have arisen along the line of mycorrhizal infection.

Still another type of mycorrhiza occurs in very many flowering plants, but seems to bear no relation to seed germination. Here the mycelium does not wind itself up in a ball-like manner in the cells, but passes through the outer layers of the root and then forms haustoria-like endings (*arbuscles*). Swollen terminal or intercalary portions of the mycelium also occur (*vesicles*). The arbuscles eventually break down,

leaving small roundish bodies full of oil. The vesicles resemble developing sporangia to some extent, and recently have been reported to produce spores, though the observation requires confirmation. The general appearance of the fungi recalls the *Phycomyces* and, if the vesicles are really sporangia, the suggestion is that the fungi are species of the genus *Endogone*, whose other members are partly or wholly subterranean.

It has been held that the possession of a mycorrhiza of this type distinguishes a perennial flowering plant such as *Mercurialis perennis* from its allied annual species, here *M. annua*, but a considerable amount of investigation is necessary before we can safely draw such far-reaching conclusions. For our present purpose it is sufficient to state that mycorrhiza of this type are exceedingly frequent in herbaceous plants, and that at present we have no certain knowledge of the benefits derived from the association by either of the components. Occasionally the balance appears to be upset and the fungus becomes parasitic; it has been stated recently that the Lanark strawberry disease is an example of this.

A further example of a union between flowering plant and fungus is seen in rye grasses (*Lolium*). Several species of this genus have a stratum of fungal hyphæ between the seed coat and the aleurone layer. When the seed germinates the fungus infects the growing point of the stem and keeps pace with its growth, but never descends far down the stem. When the ovary is formed the fungus penetrates it and thus gains entry into the seed. It seems possible that here we have a further advance along a line which can be traced among smut fungi infecting the grains of cereals. Certain species of *Ustilago* infect grass flowers and ripening grain, and in *U. nuda*, for example, the further behaviour closely resembles that of the *Lolium* fungus. At present it seems safer to assume that such

an infection has gone a stage further, the production of spores being omitted as the mycelium never leaves the plant, than to regard it as a development of a mycorrhizal infection. *Lolium* also possesses a mycorrhizal fungus of the Phycomycete type, but there is no evidence of any connection between the two fungi.

2. LICHENS

Possibly the best known intimate association of fungus and green plant is the lichen. Indeed, the lichen is the classical example of the phenomenon of symbiosis, for every lichen is a compound organism and the term was first used in this connection. It was recognized from earliest times that lichens formed a group apart, having a characteristic appearance and habitat; with few exceptions they are land plants of simple structure. When their anatomical structure began to be investigated it was realized that they consisted of two distinct portions, hyphal-like, colourless threads sometimes compacted into tissue-like masses and green or blue-green roundish or bead-like portions (*gonidia*) arranged either in definite layers or interspersed throughout the body of the lichen. The general resemblance of the coloured portions to green and blue-green algæ was realized, but the suggestion that lichens were composite organisms, the colourless portion being fungus and the coloured alga, was generally adopted only after a very acrimonious controversy, which was ended when it was found possible to build up a lichen thallus by combining fungus and alga in the laboratory.

The fungi which occur in lichens are not known in a free condition, whereas the algæ are for the most part common aerial forms which inhabit moist and shady situations, and some of the older lichenologists believed them to be escaped portions of lichens able to continue their existence. The alga sometimes under-

goes slight modification in the gonidial state, and it never reproduces in other than a vegetative manner. It is the fungus which, except in primitive forms, decides the general shape of the lichen and provides the fruit. The fungi which are found in lichens, leaving out of account some of the indefinite primitive forms, are Ascomycetes (see p. 70), with the exception of three tropical genera, *Cora*, *Corella*, and *Dictyonema*, which are Basidiomycetes; we have, therefore, the two main divisions, the *Ascolichens*, which include almost all known lichens, and the *Basidiolichens*, very restricted in number and in distribution. The lichen fruit in the main division is a disc-shaped or flask-shaped structure, essentially fungal and similar to the fruit-bodies of Discomycetes and Pyrenomycetes, the main groups of the Ascomycetes. There is every reason to believe that the association of fungus and alga to form lichen arose at least once in both these groups; in other words, that lichens are polyphyletic in origin. There are gonidia present in the thalloid margin of some fruits, but whether this is so or not it is generally possible after a little experience to decide at once on microscopic examination whether one is dealing with fungus fruit or lichen fruit.

When the spores of lichens are sown on a nutrient substratum it is difficult to entice them to grow unless gonidia are present. However, such pure cultures of the fungus have been obtained occasionally during the last forty years; growth is slow and soon ceases, continuing at most for a few months. Theoretically it should be possible to provide the lichen fungus with nutrient for its continued growth, but so far no means have been found for replacing the action of the alga. The method of dispersal by spores is therefore somewhat fortuitous, for unless the appropriate alga is encountered no growth of the fungus occurs. A much more certain method is by *soredia*, which are small

masses of gonidia surrounded by fungal hyphæ. The two symbionts are thus able again to live in union when soredia are liberated and alight favourably. Sometimes in conditions of shade and moisture soredia cover the surface of a thallus; in other lichens they are formed in definite areas which are more or less specifically constant in form, size, and position. Another way in which certainty of union is occasionally accomplished is by the breaking-off of small portions of the thallus. This method is best known in the manna lichen (*Lecanora esculenta*), where small rounded portions are blown about the desert and have been considered by some to be the manna of the Israelites.

The precise relation holding between fungus and alga is one which has been much studied, and there is much conflicting opinion. The common idea is that in a healthy lichen the alga and fungus are well balanced, and that both gain some advantage from the association. Under conditions where the lichen is not flourishing the fungus may die out, or, on the other hand, it may act parasitically—its hyphæ penetrating the walls of the algæ and bringing about their death. Normally there is no penetration of the algæ, which remain green and well nourished, and after rain, actively divide. The gonidia, owing to possessing chlorophyll, are able to form carbohydrates in the light; their general arrangement in the lichen thallus ensures that they are in the best position to make use of any light falling on it. Presumably, the fungus benefits by the passage of sugars through the algal membrane, though it should be mentioned that it has been recently stated that small granules of starch are demonstrable on the *outside* of the gonidial wall. On the other hand, the fungus probably acts by preserving the alga from desiccation by absorbing water and the necessary mineral salts, by storing water, and also by physical protection, which serves also against ex-

cessive insolation. Whatever view may be taken of the precise physiological balance struck between the component organisms of a lichen, the fact remains that lichens can be classified into families, genera, species, etc., just as if they were not composite structures; there is intimate and constant union which has as one of its consequences the possibility of recognizing wherever a particular association has occurred—a recognition which holds not only for the external morphology, but also for the most intimate details of structure.

Whatever advantage or otherwise the different components gain from the association, the compound organism is able to withstand physical conditions which neither constituent could endure uncombined, though, as has been said, we know of no lichen fungus able to continue to grow apart from its alga. On account of their property, lichens are often spoken of both as the pioneers of vegetation and the outposts thereof. For example, lichens are found in the sunniest and most arid places in deserts, being able to exist with the small amount of dew there; desert lichens are usually closely adnate to the rocks, and have a small evaporating surface, often with a thickened cortex which prevents damage from too intense sunlight. Likewise in the polar regions lichens spread extensively over rocks and stones where there is not a permanent snow covering; and lichens are to be found on the rocky summits of the highest mountains.

Lichens are the first organisms which colonize bare rock. This, which was mentioned by Linnæus, is generally recognized, but much research requires to be done to learn the details of how this is accomplished. The lichens responsible differ according to the nature of the rock and also whether there is nitrogenous matter present. They are all small crustaceous forms. By the secretions of acids from

delicate filaments, the surface of the rock is penetrated and broken down at the place of contact. A favourable rock face becomes completely covered by lichens. Later the flat leaf-like or foliose lichens appear, gaining a hold in places where some of the older thalli of the crustaceous species have died out. These more vigorous and larger lichens gradually kill off the crustaceous forms by smothering them. The sequence of colonization is continued by mosses and flowering plants gaining a footing. Granite, basalt, and lava are all prepared for higher vegetation by the activities of lichens.

Lichens are usually associated with the idea of slow growth and long life. Although, however, some lichens hardly show any advance in fifty years, the more active foliose species, particularly those occurring on the soil and consequently in a favourable position for moisture, grow relatively quickly and spread over decaying leaves, dung, and other substrata characterized by their unstability.

One of the striking features of the physiology of lichens is the production by most species of "lichen-acids," many of which occur nowhere else in nature. They are to be seen as minute crystals or granules on the outer surface of the hyphae. So far as is known, these acids, which are often brightly coloured, are formed only in the lichen plant and do not occur when either the alga or the fungus are grown separately. Some acids apparently occur only in one, or at most in very few, species. The bright colour of many species due to these acids was doubtless the reason for the use of lichens as dye-plants in antiquity; the "blue and purple" of Ezekiel probably refers to lichen dyes, and the account by Theophrastus and Pliny of the dyeing of garments in Crete certainly does. Most works which mention lichens have dealt with the preparation of dyes of all colours from yellow to purple, and the species from which they can best be

obtained. One of the best known dyes is litmus, and the variety of colours that can be secured is well shown in the famous Harris tweeds.

Lichens are occasionally used as food by man, and reindeer moss (*Cetraria rangiferina*) is well known as the food of reindeer. Lichens were formerly much used in medicine, the common *Peltigera canina* being reputed a certain cure for the bite of a mad dog.

CHAPTER VI

FUNGI AND INSECTS

THE relations existing between fungi and insects are variable and offer many problems of the greatest interest. Insects play a part in the dispersal of fungal spores. Many fungi of the group represented in this country by the stinkhorn (*Phallus*) produce their spores embedded in a glutinous mass which is rarely anything but evil-smelling. This is attractive to flies, which, eating the material, serve to distribute the spores. In addition to this there is a casual transport of spores by insects which, crawling over plants, become dusted with the spores and so carry them to other plants. If the second plant is the same species, the spore of a parasitic fungus is often carried to the same organ and, being in a suitable position, may cause disease.

A common indirect result of insect action is seen in the black, sticky coverings of elm, lime, and other trees. Aphides puncture the leaves, absorb plant juices, and emit the sugary "honey-dew." This is a suitable pabulum for the development of black budding fungi of the yeast-like type, the commonest in Europe being *Dematium pullulans*, though other sooty moulds occur.

Entomogenous fungi, parasitic on various insects, are far from rare. The common house-fly, surrounded by a sort of halo, may frequently be found in autumn attached to a window-pane. Fly cholera, as it is sometimes called, is due to the fungus *Empusa Musca*, one of the Phycomycetes. The spores germinate on the

body of the fly, penetrate to its interior, and there form a mycelium which, by its growth, eventually kills the fly. The hyphæ then penetrate the integument and constrict spores, which are shot off and compose the halo. Other species of *Empusa* and an allied genus *Entomophthora* are not uncommon on Diptera.

Cordyceps is another well-known entomogenous fungus. The common species in Europe is *C. militaris*, which occurs mainly in woods and hedges as a small scarlet club proceeding from an underground caterpillar or cocoon. The top of the club is finely punctate, the punctations marking the exits of flask-shaped cavities in which are borne clavate asci, each containing eight spores. Another stage of the fungus is perhaps more commonly found. This is white, powdery, feathery, and upright (*Isaria*). The spores here are borne directly on the hyphæ. (The occurrence of two stages of different appearance and structure is very common in fungi. The stage containing the sexual stage, or the place where this presumably previously occurred, is known as the perfect stage; the other, which represents a vegetative method of reproduction amounting merely to a budding off of the ordinary mycelium, is the asexual or conidial stage. The conidium usually serves as a means of rapid spread for the fungus, whereas the sexually produced spores are able to overwinter.)

Species of *Cordyceps* occur on every group of insects. The mycelium of the fungus, having gained admittance, fills the interior of larvæ or pupæ, which have buried themselves in wood or in the ground to complete their metamorphosis. The clubs arise from the sclerotium-like mummified caterpillar. The occurrence of fungi of this type has always excited wonder. A West Indian species of "vegetable fly" was described in 1763. "In the month of May it buries itself in the earth and begins to vegetate. By the

latter end of July the tree arrives at its full growth, resembles a coral branch, is about three inches high, and bears several little pods, which, dropping off, become worms, and from thence flies, like the English caterpillar."

The best known species, the "vegetable caterpillars" of Australia and New Zealand, may reach a height of over a foot. The "summer plant, winter insect" of the Chinese Pharmacopœia is of great repute. It is brought into Canton in bundles of about a dozen tied up with red silk thread. Accounts vary about its frequency. Some say it is sold as food, but the usual statement is that it is so rare, being found only in Thibet and the outlying parts of the Empire, that its use is restricted to the Emperor's physicians, who administer it with roast duck; black, old, and withered specimens are said to be the most valuable, and worth four times their weight of silver.

The Laboulbeniales are a fairly large family of minute Ascomycetes, which are confined to the chitinous integuments of living insects, usually appearing to the naked eye as dark coloured or yellowish bristles. They apparently never give rise to epidemics. They are of great academic interest, many botanists regarding them as showing phylogenetic connection with red algæ.

Fungi parasitic on insects are of importance on account of their possible economic uses. Insects frequently cause great damage to crops, often vying with fungi in the amount of destruction they bring about. Metchnikoff, in 1878, finding that cockchafers which caused disease in wheat were themselves killed off by a fungus (*Isaria*), cultivated this and attempted to spread the infection, an experiment which has been repeated. The fungus was afterwards found to affect silkworms, causing the troublesome green muscardine. Similar attempts to use parasitic fungi for killing off troublesome insects have been made frequently. The

rhinoceros beetle, which attacks coconut palms in Samoa, is also parasitized by a species of *Isaria*. It has been recommended to sow spores of the fungus in refuse heaps so that the larvæ would be attacked when they hatched out from the eggs laid there.

Chinch Bug, which is a serious pest of grain in North America, was so destroyed by a mould (*Sporotrichum*) in 1865 that scarcely one thousandth of the vast hordes survived. Epidemics recurred at intervals, and in the nineties an experimental station was established for the purpose of investigating the possibility of using the fungus on a large scale for artificially producing similar epidemics.

In recent years this method of dispatching troublesome insects has been recommended chiefly for getting rid of white fly in the citrus groves of Florida. This insect causes little direct damage, but by its emission of honey-dew, provides food for black, disfiguring sooty moulds. Experiments have been carried out with various natural parasites.

When the recorded results are analyzed, the impression left is that the often repeated claims for the success of the method are unwarranted. An artificial epidemic can always be produced in cage experiments, but when inoculation is tried in natural conditions it does not have the same success. There is always a certain amount of natural infection of these insects, and this reaches an epidemic form when conditions either particularly favour the fungus or are detrimental to the insect. When an attempt at artificial infection synchronizes with a wave of natural epidemic, apparent success of the method results, whereas all that has been accomplished is presumably a hastening of an inevitable result.

To many, the most fascinating relations between fungi and insects are those which may be conveniently classed together as symbiosis, so long as the term is taken to mean nothing more than that there appears

to be a constant obligate association. Two main types occur. In the one, the fungus is external to the insect, in the other it is internal. Both these types exist in many groups of insects which are not closely related, and it seems clear that they must be of independent origin; in other words, the special relations which we are considering have arisen time and again in the evolution of insects.

The fungus-gardens of the leaf-cutting ants of South America have aroused interest ever since Belt expressed his belief that they were "mushroom growers and eaters." Most travellers have described the processions of these ants, how they climb and defoliate trees, cross streams and anything that is in their path, and march like an army, bearing aloft their portions of leaves like so many bannerettes. All the fungus-cultivating ants are American, and mostly tropical. They number about a hundred species, and there is much variety in the nests, in the way they are made, and in the forms of the ants. Only a generalized account can, therefore, be attempted. When the ants arrive at the nest with their leaves these are taken over by workers and cut into pieces which are sufficiently small to be worked up into a pellet. This is placed in the fungus-garden and soon becomes permeated by mycelium. The fungus-garden is definitely cultivated, and produces abundant clusters of small, spherical swellings, *bromatia*, upon which the ants feed and also nourish their larvæ. Each species of ant apparently cultivates its own particular fungus. If the ants are removed the production of *bromatia* ceases, and, so far, no attempt to produce these artificially in cultures of the fungus taken from the nest has succeeded. Möller believes that the fungus cultivated by *Acromyrmex* is a toadstool (*Rozites*) mainly because, on four occasions, he found the same species growing from the centre of abandoned nests. More recently other toadstools have been described from nests, the

most remarkable being a species of *Locellina*, with a cap more than 40 cms. across.

The starting of the fungus-garden is not left to chance. The virgin queen, before leaving the nest on her nuptial flight, indulges in a substantial meal of the fungus, and carries it away as a pellet packed into her infrabuccal pocket. She retains the pellet until after mating. Then, after discarding her wings and making a small chamber in the soil, she ejects the pellet and begins to lay eggs. The queen deliberately manures the fungus with her excrement, and even breaks up some of her eggs to provide it with additional nutriment. The mycelium is so arranged that it forms a nest for the remaining eggs. When the larvæ hatch out they feed on the fungus and eventually pupate as workers. Some of these tunnel to the surface and bring in pieces of leaves to add to the garden. There are other ant-fungus associations which, though not so picturesque as the one just described, suggest problems of great biological interest.

Another group of insects which cultivate fungus-gardens are termites or white ants. These insects are notorious for their insatiable appetite for cellulose in any of its forms—wooden structures and books included. Cellulose, however, is not a very highly nutritious or digestible food, and insects which feed on it have either to pass enormous quantities through their intestinal tracts or make use of the activities of other organisms. The more highly evolved species of African and Indo-Malayan termites with elaborate nests bring this about for their young by the aid of fungi; the others possess intestinal protozoa.

Fungus-gardens were first noted by Koenig about 150 years ago, but their significance was not understood until comparatively recently. The comb of the nest is formed of wood which has been passed through the intestine of termites. It is hoary with a covering of short fungal hyphæ, which bears minute white spheres about

the size of pin-heads. It has been shown by feeding experiments and by dissection that these spheres are the termite food. The fungus-gardens are really the nurseries, and are full of newly hatched young which feed on the spherical bodies. The king and queen and other reproductive forms are also fungus eaters, but the soldiers and workers obtain their food on excursions from the nest. Occasionally the fungus gains the upper hand and the fruit-body of a toadstool appears (*Collybia*). It is the best known edible fungus in Ceylon.

Beetles also make use of fungi for digesting cellulose. The name *ambrosia* was given almost a century ago to a fairly thick lining in the burrows of certain beetles and used by them for food. Shortly afterwards it was recognized that ambrosia was a fungal growth. There are about 400 species of ambrosia beetles. They attack healthy or recently felled trees, running burrows into the sap-wood and then excavating at right angles to this along the annual rings. The eggs are laid in these side passages and arranged in different ways according to the species. The walls of the chamber become lined with a growth of fungus, which often gives it a black stain. The larvæ feed on the fungus, which is sometimes placed conveniently for them by the mother. It has been stated that the pellets of larval excrement are used by some species for manuring the fungus. The swarming female carries the fungus with her either in the fore part of the stomach or in a kind of basket formed of tufts of long curved hairs on top of her head or on her mouth parts. The fungus is of the budding type similar to a yeast (*Endomyces*). A similar fungal lining occurs inside plant galls caused by gall midges.

One of the most unexpected relations between fungi and insects has been brought to light during the last few years. Fungi, particularly yeasts, are known to occur constantly in numerous insects, the fungus, or fungi, always being the same for a particular insect

and always occurring in the same situation. Most of these fungi are not known in a free living condition. Various bodies were frequently described in coccids and other insects from about 1850 onwards, but though it was several times suggested that these were,* in reality, fungal cells, and even that they were symbiotic, it was not until 1910 that Sulç and Pierantoni independently pointed out their true nature. These fungal cells occur in large numbers of insects and differ both in arrangement and in complexity. As with other kinds of fungus-insect relations, we are forced to believe that the association did not arise once for all and so allow us to arrange a theoretical evolutionary series of increasing specialization, but that the step has been taken many times, and for the most part is independent of the ordinary phylogenetic progress; the associations have nothing in common except a similarity of function.

The simplest arrangement is where, as in coccids (*Lecanion*), the fungi are scattered throughout the body. In the biscuit beetle (*Anobium*) the yeasts occur in a special region of the intestinal epithelium; the relation is here rather exceptional, for the yeast is not passed on by entering the egg, but has to be acquired by the larva. Most frequently the fungi are contained in special cells (*mycetocytes*), which are usually agglomerated to form tissue organs (*mycetomas*). There are many variations in their arrangement and in the fungi they contain. Bacteria also enter into similar association with insects, and they may occur alone or together with fungi. Some insects have both a differentiated mycetoma and scattered mycetocytes, each structure with a different fungus; some have two separate mycetomas with different fungi, others have fused mycetomas, and so on. As many as three distinct fungi have been described as normally present in certain insects.

What advantages are gained by the two different

constituents of this peculiar association, which we must consider normal, for there are special contrivances for ensuring its continuance? The fungi apparently find a suitable habitat and satisfactory means of dissemination. On the other hand, the insect appears to be able to benefit through being able to utilize various substances for nutrition which would otherwise be worthless to it. The fungi have every appearance of fulfilling important physiological functions. Many insects which harbour them are plant parasites. These extract plant juices, which are fermented by the yeasts: the structure of many mycetomas allows of the ready gaseous exchange which is necessary for the process.

The fungi which occur in tsetse flies, the carriers of sleeping sickness, are supposed to be correlated with the blood-sucking habit, possibly possessing enzymes, which aid in the digestion of albumen and other blood substances. Closely related non-blood-sucking forms are apparently without internal yeasts.

The relation between fungus and insect appears to be a well-balanced one, for, so far as we know, the fungus never gets out of hand and causes damage. This is surprising, for in many ways they are much like the yeast which Metchnikoff described as killing the water flea—a research of great consequences, for it led to his discoveries of the work of the white corpuscles of blood (phagocytosis).

CHAPTER VII

ECOLOGY AND CLASSIFICATION

It now only remains for us to consider an outline of the distribution of fungi and their classification. Something has been said of the former, but a few points need to be added to complete the picture.

What has to be visualized is a group of organisms dependent on other organisms for their existence, an enormous and virile group ready, as it were, to snatch at any food which will sustain them. Occasionally they pay the price of the risks they take and become chained to some other organism to aid it in its life struggles, sometimes apparently receiving some benefit in return, sometimes apparently being discarded when their usefulness is at an end. All food, in fact all organic material, is liable to be destroyed by them—bread, cheese, jam, and fruits become mouldy; cloth and fabrics are marked and spoiled; wood is reduced to powder; wine, beer, and milk also have their “diseases.” Endless destruction of what man prizes is due to these organisms, and he, his crops, his trees, and his animals do not escape attack.

That is one side of the picture. On the other, we have fungi sharing with bacteria the work of scavengers and converting organic remains into food substances available for higher plants. For example, it is now known that there is an abundant mycological flora of the soil, many fungi apparently carrying out the whole of their life-cycle there. The most important work they do is breaking down the refractory cellulose of the remains of stems, roots, leaves, and wood, and thus

rendering the soil fertile. It is difficult to imagine what would be the immediate result if decay ceased; ultimately life itself would be impossible.

The geographical distribution of fungi is in outline much like that of other organisms. Some species are cosmopolitan, whereas others are endemic to restricted areas. Generally speaking, saprophytic fungi are found in definite situations as, for example, in water, on wax, resin, and burnt ground, and, as we have seen, parasitic fungi are often strictly confined to their hosts. When the organisms of a natural habitat are studied it is found that fungi play a definite part and fit into the general scheme. Pastures, heaths, and woodlands of all kinds have certain characteristic species which as, for instance, in coniferous and beech woods, where the dense canopy interferes with the development of a ground flora, are much more numerous than are herbaceous plants.

It is not possible to give more than the barest outline of classification, for fungi are an enormous and complex group. There are two main objects in view in attempting a classification; the construction of a natural system and the identification of individuals. We usually talk about the construction of a natural system as the main object of classification, the arranging of species into genera, of genera into orders, of orders into classes, of classes into divisions in such a way as to show relationship. It is obvious, at first glance, that some fungi are very closely related, as, for example, the field mushroom and the horse mushroom. A little observation reveals that many other fungi show similarities with these. With more knowledge of structure we recognize an ever widening circle of affinities, and we are able to enlarge and also to subdivide our sections. Clues of all kinds add to our certainties and modifications are made here and there. This will continue until eventually we shall have, theoretically, a complete scheme with all its parts interrelated, and the

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whole displaying an epitome of mycological knowledge.

The idea of a natural system is not new, but the general acceptance of the theory of evolution gave an impulse to the academic aspect of classification. This explained the possibility of a natural arrangement as due to related forms having had a common descent. Whether this is the real explanation or not is considered in other books of this series. What should be understood, however, is that the modern system of fungal classification had its origin in pre-Darwinian days, and that only in the broadest sense can it be said to have been influenced by any doctrines of evolution. By noting similarities of structure, development, cytology, physiology, and so on, it is possible to come to a definite opinion that certain fungi are very closely related—*i.e.*, that they are most reasonably and conveniently placed together in the system of classification, their position with regard to one another depending upon the degree of similarity. For convenience these could be arranged either to show increasing complexity or the reverse. Accepting the doctrine of evolution we are able to assume what has been the probable order of development.

The more immediate object of classification, that of identification, is frequently lost sight of. It is impossible to lay too much stress on the necessity for correct identification, for no general conclusions of any kind are of the slightest value if they are founded on a misidentification. Some kind of system is needed by which to find a way about the maze of forms. By the use of properly constructed dichotomous keys it is often possible to reach correct determinations, and doubtless a purely artificial classification based on differentiating characters might prove as accurate as a natural system taking account of the whole of the characters. The end in view is usually not merely to find out the name of a fungus, and the proper understanding of a natural

system often gives a clue to the further knowledge we are seeking. Thus, for example, if the fungus is a disease-producing organism an indication of a possible method of successful treatment is often gained by ascertaining its systematic position and learning the characters of its allies. Moreover, an early identification of a fungus opens the way to all that has been written about it.

Though there are several systems of classification of fungi, they differ mainly in details. The search for an absolutely natural system is a constant stimulus to systematists. It is a search which is still in progress, and though it is more than probable that we shall never achieve finality, there is always the possibility of carrying it a little further towards perfection. Some systematists are engaged in describing more and more species, a necessary but often much criticized activity. Others work on broader lines, filling in the gaps, and by intensive studies gain a surer basis on which we may gradually build up a logical system.

In beginning the study of a fungal classification it is best to concentrate on the broader lines and to study what may be considered to be typical forms. Systematy, as we know it, has had the same sort of gradual development as have had other branches of science, and it is difficult without some previous knowledge to understand why some of the simpler forms usually considered as the most primitive are placed in a given group. Consequently, these often rare types which, on account of their phylogenetic interest figure largely in textbooks, are best left for later study.

The three main divisions of fungi are PHYCOMYCETES, which resemble green algæ in structure, typically filamentous and having large and well-defined sexual organs which give rise to thick-walled zygotes directly after fertilization; ASCOMYCETES, which usually form definite fruit-bodies containing subglobose, or clavate sacs (*asci*), in which spores are formed, usually to the

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number of eight, and BASIDIOMYCETES, also usually with definite fruit-bodies, but with their spores, usually four, borne on *basidia*.

In addition to these there are the innumerable and important FUNGI IMPERFECTI. Many fungi are pleomorphic—that is, they have more than one stage in their life-cycle. Sometimes there is no doubt about the connection between the stages, because they occur together on the same mycelium. The stage of the fungus life-cycle, which contains the zygote, the ascus, or the basidium, is known as the perfect or sexual stage, as sexuality, or what replaces it, results eventually in the formation of these structures. The other stage, the conidial, imperfect, or asexual stage, is independent of sexuality, and usually serves for the rapid spread of a fungus. Spores (*conidia*) are budded off from a mycelium, which may be free (Hyphomycetes), enclosed in a flask-shaped pycnidium (Sphærospideæ), or form a compact layer which may be surrounded by a pseudo-membrane formed by the upraising of the epidermis of a host plant (Melanconieæ). The conidial stages of Phycomycetes are not included in the classification of Fungi Imperfecti, because, being very characteristic and often recognizable as belonging to a given genus, there is usually no doubt about their proper place in the general system. The assumption is that the other forms all have Ascomycete or Basidiomycete connections. The general name Fungi Imperfecti is given to them, because their life-cycle is incompletely known, though it is possible, and apparently the more commonly accepted view, that they have an incomplete life-cycle owing to the dropping out of the perfect stage. Mycological textbooks usually devote little more than a few lines to their treatment, though, as large numbers of them are plant pathogens, they are of great importance.

PHYCOMYCETES first received their name from the belief that they were degenerate green algæ. They

may be divided into Chytridiaceæ, Oomycetes, and Zygomycetes. The Chytridiaceæ comprise the simplest forms, often consisting merely of a single cell, which may or may not possess a cell-wall. So far none have been described which are motile throughout their vegetative life, but the majority of them propagate by means of motile spores (*zoospores*), which are formed from the whole or from part of the vegetative body. They are able to swim about by the movement of their protoplasmic extensions (*flagellæ*) which are either one or two in number. Usually these fungi live parasitically in the cells of green algæ or in the roots of marsh plants, though some occur in leaves. The best known is *Synchytrium endobioticum*, which attacks potato tubers and causes the destructive wart disease. As we have seen, one of the most marked characteristics of fungi in general is the possession of a thread-like mycelium, which absorbs nutriment for the developing fruit-body. We can trace a gradual development of mycelium in the Chytridiaceæ, the simplest forms being without any. Various other evolutionary tendencies may be made out, but, generally speaking, these fungi are of interest only to the specialist and, except where they occasionally cause disease, do not come to the notice of the general public. Both Oomycetes and Zygomycetes possess a well-developed mycelium, which, typically, is wide and without divisions except where some process of reproduction is in progress: the mycelium acts both as an absorbing organ penetrating the substratum and as a spore-bearing structure. The main difference between the two orders is in the sexual organs. Oomycetes possess well-marked male and female organs (in one family having motile male gametes), whereas Zygomycetes have fusing branch ends which usually show little differentiation. There are many points of great theoretical interest in the details of sexual reproduction.

Correlated with the difference in the sexual stages,

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there are differences in the asexual stages. Roughly, these are that Oomycetes have zoospores, or aerial zoosporangia ("conidia") borne freely on the mycelium, while Zygomycetes have their asexual spores borne within a sporangium which is essentially the swollen end of a hyphæ. Here, again, we have a series of differences which are useful for systematic purposes, and presumably have phylogenetic significance. A change from an aquatic to a land habit may be traced in Oomycetes. The only family with spermatozoids (Monoblepharidaceæ) has also zoospores and its members occur in water. *Saprolegnia*, which forms the woolly tufts so frequent on ornamental fish, and its allies have zoospores, but sexual reproduction is by the fusion of an antheridium and an oogonium, a method found throughout the rest of the group. *Phytophthora infestans*, the cause of the potato disease, shows the next stage where "conidia" are formed freely on hyphæ standing upright from the under surface of the leaf. These drop off and are blown about freely, and rapidly spread infection. Damp conditions greatly favour the disease, because the conidia, on development, produce zoospores which need a film of moisture for their activities. The change from the sporangium to a true conidium is gradual, and sometimes the structure acts as one or the other according to surrounding conditions. It is rare for true conidia to be formed invariably. The group is responsible for the diseases known as downy mildews which affect vine, lettuce, and other crops; they also cause "damping-off" and many other well-known diseases. Zygomycetes, on the other hand, are mostly saprophytic, being frequent in the soil and on foodstuffs. Typically, as in the common bread mould (*Mucor*), numerous spores are produced in a sporangium, but we have various modifications of this. Along one line of development in the order the sporangium contains fewer and fewer spores, until it

becomes monosporous, and finally a conidium; along another line we have late spore formation occurring in projections of the wall of the sporangium, then a reduction in the size of the sporangium, and finally a breaking up of the external portions until there is what amounts, in appearance, to a conidiophore, though its origin is very different from what occurs in Hyphomycetes.

Ascomycetes are a much larger and much more varied class than Phycomycetes. Here the mycelium is usually much narrower, has numerous septa, and generally is compacted into a definite fruit-body. In the simpler forms, the asci have no definite arrangement, and they are usually small and more or less globose. The asci of the more complex forms are larger, club-shaped and arranged in a definite layer, the *hymenium*, frequently with interspersed sterile cells, *paraphyses*. The modern classification of Ascomycetes is very complex. It is best approached by considering those forms with a hymenium. Where the hymenium is exposed from the beginning of its development we have the old group DISCOMYCETES, so named because its typical members are cup-shaped with the hymenium lining the inner surface of the depression. Here are included the morels (*Morchella*), which have a stalk surmounted by a conical head with a honeycomb-like surface, the hymenium lining the hollows. In the other main group, known as PYRENOAMYCETES, the hymenium lies inside flask-shaped structures (*perithecia*), which have a small opening at their summit. They are a much more diverse group than are Discomycetes, and far exceed them in numbers. Many of them are important plant pathogens. The perithecia are sometimes free, but more often are formed within a mass of compact tissue-like mycelium called a *stroma*, which is occasionally of large size. Ergot (*Claviceps purpurea*), which is common on grasses, is typical of these. Ergot of rye

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formerly caused gangrenous disease in man and animals, usually in times of famine, but modern rapid transport has stifled its ravages. As the grass flower opens it is infected by the spores of the fungus, and soon the ovary is a mass of hyphæ. These produce conidia and a sugary secretion attractive to insects, which spread infection from flower to flower. Later, the mycelium becomes converted into a hard, purplish-black sickle-shaped sclerotium, which projects from the inflorescence. After a time this ergot falls to the ground and lies dormant until spring. Then it begins to grow and forms two or three drum-stick shaped stromata with perithecia embedded in the spherical head. The ascospores are liberated about the time the grass is in flower, and, blown on to the stigma by the wind, cause infection.

Many Ascomycetes have fruit-bodies which have no opening, and need to break apart for the liberation of spores. They are a heterogeneous group, and some of them are of great phylogenetic interest. The powdery mildews, such as those of the rose and the apple, are representatives of one section, the small yellow fruit-bodies (*Eurotium*) on jam of another, and a third includes some of the truffles. On the other hand, we have some Ascomycetes with no fruit-bodies. The best known of these are yeasts which, when conditions are unfavourable for rapid vegetative increase by budding, become converted into asci containing one or more spores (endospores = ascospores).

There are many interesting problems of sex and development in the Ascomycetes. Some of the primitive Discomycetes show well-marked male (antheridia) and female (oogonia) organs; in other species, presumably more advanced, we have an oogonium but no antheridium, while in the majority all trace of both is lost. We are still uncertain about the precise details of the sexual process.

The final class is the BASIDIOMYCETES. The mycelium

is usually narrow, with many divisions, being much like that of Ascomycetes. As understood here, it is a heterogeneous class, including mushrooms and toadstools, bracket-fungi, rusts, and smuts, the character in common being the possession of a basidium or its equivalent.

In the common mushroom (*Psalliota campestris*) there is a cap (*pileus*) borne on a stalk, adorned a little above the middle with a ring of tissue, which is joined to the cap in the early stages of development. On the under side of the cap radiating plates of tissue occur. These *gills*, when sectioned, show crowded ranks of club-shaped basidia spaced by sterile paraphyses. The basidia bear two spores on teeth-like projections, though four is the usual number in Basidiomycetes just as eight is in Ascomycetes. An interesting point is that just as the spores are ripening a minute drop of water appears at the point of junction of the spore and basidium, and is carried away with the spore when this is violently shot off.

In the classification of toadstools the characters of importance are the colour of the spores (white, pink, brown, purple, black), the mode of attachment of the gills, the presence or absence of a ring on the stem, or a cup-shaped *volva* which originally enclosed the whole fruit-body. These, together with consistency—i.e., whether the fungus revives after drying—are by their permutations and combinations sufficient to enable us to distinguish most of the genera. The gills and cap of most species of the genus *Coprinus* undergo autodigestion after spore discharge, and as the spores ripen from below upwards the zone of discharge is followed by "deliquescence."

The hymenium, instead of clothing gills as in the *Agaricaceae*, may line the inside of tubes as in *Boletus* (*agaricus*) and many of the destructive bracket-fungi occurring on tree trunks (*Polyporus*). Again, the hymenium may be on spines (*Hydnum*), or club-

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shaped sporophores (*Clavaria*), or be even or corrugated as, for example, in *Stereum purpureum*, which causes "silver-leaf" in plum-trees. All these different types which have their spores freely exposed long before their discharge form the old division Hymenomycetes. The other large group, Gastromycetes, which includes the puff-balls, earth-stars, stinkhorns, etc., has the spores enclosed by a membrane until they are mature; they are liberated after the rupture of the membrane.

The general life-history of a rust fungus was considered in the chapter on Plant Pathology (see p. 38).

The inclusion of smuts amongst Basidiomycetes is much more difficult to understand, and depends to a large extent on abstruse resemblances in development. They are all parasitic, but many pass part of their life-cycle as saprophytes, and some of them are able to carry out the whole of it in artificial culture. The smut of cereals, causing the production of a black powdery mass in place of the grain, has been known since antiquity, but many species are only to be recognized by experience. In *Ustilago Avenæ*, the covered smut of oats, the seedlings are infected through the first sheath leaf. The mycelium then grows through the plant until the flowers are formed, when it enters the ovaries and forms a mycelial mass, which soon becomes converted into spores. These are homologous with the teleutospores of rusts. They readily germinate and produce a short tube, which is divided by cross-walls into four cells, from each of which a sporidium is abstricted, which, under favourable nutrient conditions, buds in a yeast-like manner. This production of sporidia corresponds to the formation of basidiospores. The sporidia frequently fuse in pairs, a phenomenon of importance in bringing about a change in the nuclear conditions of the mycelium, and the fusion product puts out a germ tube, which infects its host plant.

The classification here summarized is the one adopted in most systematic works, but has been modified somewhat in recent years.*

This introductory outline of mycology would hardly be complete without a reference to the subject of homothallism and heterothallism. The vegetative body of algæ, fungi, and lichens is termed a *thallus*, as there is no differentiation into stem and leaves. Homothallism, therefore, signifies in a fungus that all mycelia are of one kind, heterothallism that different kinds of mycelium occur. About fifty years ago the fact was often remarked that some Mucorineæ frequently produced zygospores whereas others rarely did so. Early in the present century Blakeslee discovered the reason of this. Some species like *Sporodinia grandis*, a common mould on toadstools, will form zygospores if a single spore from a sporangium is grown in culture; others, however (*Mucor* spp.), form only sporangia no matter on what medium they are grown and under what conditions. If, however, numerous mycelia obtained in this way are grown in pairs, it is found that at the line of junction of some of them zygospores are produced in abundance; there are two different types of mycelium. These different mycelia are usually labelled plus and minus, though there is no obvious difference between them as a rule. By a series of experiments where imperfect hybrids have been formed it has been possible to correlate the signs in a large number of species. Within recent years a great extension of our knowledge of heterothallism has taken place. The occurrence of different strains has been recorded in the Oomycetes, Yeasts, Discomycetes, Pyrenomycetes, Smuts, Rusts, and Basidiomycetes. Without entering into details we may say that heterothallism is now

* A synopsis of Engler and Prantl's classification will be found in an Introduction to Botany, No. 118.

known to occur in some form or other throughout the fungi. At first, as in Mucorineæ, it seemed that the phenomenon was purely a sex one, but the results obtained in Basidiomycetes are difficult to explain. Here, in the most complicated example, the four spores taken from a basidium all behave differently. They comprise two fusing pairs, which are intersterile, or, on the sex hypothesis, four sexes. In addition to this, it has been found that mycelia produced from single spores of the same fungus from different regions are also intersterile.

A knowledge of heterothallism has already proved useful in explaining the occurrence of some Fungi Imperfecti, though it is far too early to see whether any reasonable proportion of these are (+) or (-) strains, requiring only their mate to reveal their true affinities. It seems certain that when we have analyzed the mass of information which is rapidly accumulating we shall have much clearer ideas about sexuality in fungi—a subject which has interested investigators for many years—and its relation to certain aspects of physiology. The present position may, perhaps, be summarized thus: we have different strains of some fungi which must be present under conditions of culture before the perfect form of the fungus is produced; sometimes there are two strains, and these apparently represent male and female in certain forms; sometimes there are four strains (with geographical races) which may be sex strains, though we have yet to ascertain the true relation between them. There is some evidence that in heterothallic species the presence of the one strain is necessary for some physiological change in the medium, without which the life-cycle of the fungus is not completed. Fundamentally, sex is physiological. What we have to ascertain is whether the action of one strain upon another is of the physiological kind so far regarded as sex; if it is not, what relation, if

any, it bears to sex; and if it is sex, what is the significance of more than two sexes together with the existence of geographical differences in their action. It is possible that fungi, having developed along independent lines, may have evolved a procedure not to be matched amongst plants and animals.

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MYCOLOGY is a subject of so many aspects that few, if any, textbooks give an adequate representation of it. Much information is to be obtained only from original papers, and these become more and more numerous every year. Additional information on most of the points treated in the previous pages can be found in the following books, most of which have references to original papers :

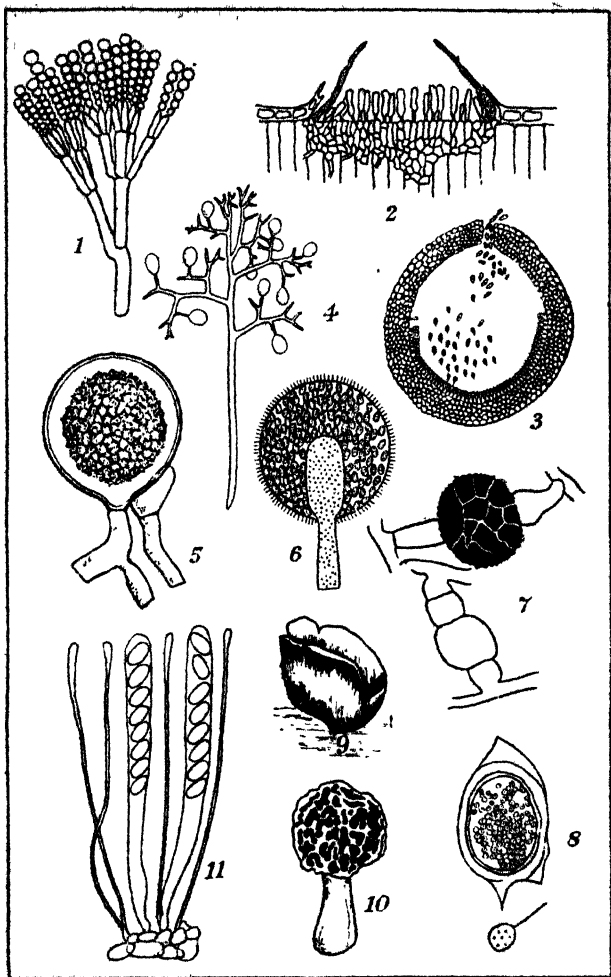
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EXPLANATION OF FIGURES

1. *Penicillium* (Hyphomycete, p. 67).
2. *Colletotrichum* (Melanconicæ, p. 67).
3. *Phoma* (Sphærospideræ, p. 67).
4. *Peronospora* (Oomycete, p. 68); conidiophore.
5. *Peronospora*; oogonium and antheridium.
6. *Mucor* (Zygomycete, p. 68); sporangium.
7. *Mucor*; Zygosporangium formation.
8. *Synchytrium* (Chytridiaceæ, p. 68); "sporangium" and zoospore.
9. *Peziza* (Discomycete, p. 70).
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12. *Claviceps*; sclerotium bearing fruit-bodies.
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14. *Sphærotheca* (powdery mildew, p. 71); fruit-body showing single ascus.
15. Yeast (p. 71) showing budding cells and endospores.
16. *Amanita phalloides*.
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18. Section of hymenium of Basidiomycete showing basidia and spores (p. 72).
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20. Rust fungus; uredospore.
21. Rust fungus; teleutospore.
22. Rust fungus; germinative teleutospore showing promycelium (basidium) with spores.
23. Smut fungus (p. 73); germinating spore.

Figs. 9, 10, 16, and 17 are much reduced; all the others except Fig. 12 are highly magnified.



For explanation, see opposite page.



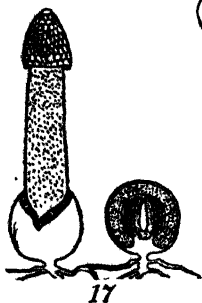
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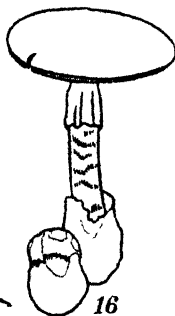
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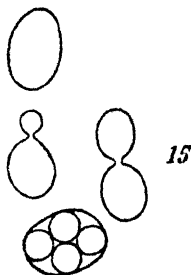
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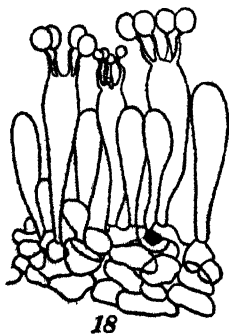
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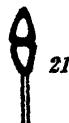
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For explanation, see page 78.

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CHAPTER I

INTRODUCTORY

THE social insects in general, and ants in particular, are, with birds and with man, the fine flowers of the tree of life. Had not their advance to greater size and strength been checked through limitations inherent from the first in the fundamentals of insect organization, they might well have evolved into beings so formidable as to have held the vertebrates back in their conquest of the land, and for ever prevented the development of man.

Innumerable comparisons have been made between human society and the social organization of ant, bee, or termite; theories have been advanced and morals pointed, Utopian schemes encouraged and whole theories of the State built up for man on the basis of analogy with these little insects. Almost without exception the moral has been false, the analogy used misleadingly. It will be well to point out at the start some of the radical differences between social insects and social man.

In the first place, the development from non-human to human mammal has occurred but once,* while the

* There are still one or two authors who uphold the polyphyletic, or multiple, origin of man. It is, however, extremely improbable that they are right; and even if they were, they only suppose that the different races of man have evolved from different types within the one small group of anthropoid apes. The multiple origin of social insects is an origin from a number of quite separate and radically different orders or sub-orders, as different as rodent from carnivore, as elephant from ruminant.

transition from non-social to social insects has occurred on a number of separate occasions. Three main grades of social habit may be distinguished. In the lowest there is some sort of a family life, either the mother or both parents living with and helping the developing young. This may be called the subsocial, or family, grade. The second is the true social, or colonial, grade, in which the young, when fully grown, stay with their parents and co-operate with them in building the nest and caring for further broods of young. The highest grade is that of the caste-society, in which some of the young are transformed into unsexed "neuters," who take off the shoulders of the fertile caste all the duties of the colony, save only that of reproduction.

According to W. M. Wheeler, the great authority on the biology of these animals, some grade of social life has been reached no less than twenty-four times in the evolution of insects, among the representatives of five separate orders. If we deduct the merely subsocial types, ten separate attainments of the true social level remain, distributed between the orders of Hymenoptera and Isoptera. Among the Hymenoptera, Wheeler believes that full social life has been acquired five separate times by wasps, three times by bees, and once by ants. Even if we suppose that ants—all members of which are social—arose as an offshoot of an already socialized wasplike form, it is at least certain that bees and wasps have developed their extremely similar societies quite independently of each other; and, in addition, the caste-system has been evolved at least two or three separate times in wasps, and at least twice among bees; finally, the Termites have developed social life and a caste-system quite separately from the Hymenoptera, and along rather different lines.

An even more striking difference between social insects and man concerns the number of species of the two types which exist. There is but one human species

now extant. Even if we take all known fossil forms into account, we can only muster half a dozen at the most. Of fully social insects, on the other hand, there have been described about 800 species among wasps, about 500 among bees, over 3,500 among ants, and over 1,000 among termites—nearly 6,000 in all; and when we reflect that systematists are discovering scores of new species, notably from the Tropics, every year, we shall probably not be making an over-estimate if we say that 10,000 separate species of social insects are in existence.

The reason for this is partly, though not mainly, to be sought in another biological difference between man and the social insects. Man dates back certainly no earlier than the Pliocene;* and *Homo sapiens* appears to have arisen only during the Pleistocene, less than one million years ago. Social ants, bees, wasps, and termites have all been found in Baltic amber, which exuded from pines growing in what to-day we call Sweden, right back in Lower Oligocene times, about thirty million years ago. In Wheeler's own words, "My study [of these ants trapped in that long-ago resin] showed conclusively that the ants have undergone no important structural modifications since the Lower Oligocene, that they had at that time developed all their various castes . . . that they attended plant-lice, kept guest beetles in their nests, and had parasitic mites attached to their legs in the very same peculiar position as in our living species." Many modern genera were already in existence, and some of the Oligocene species were practically indistinguishable from those of to-day. Typical ants have been found in the Eocene, and the strong probability is that several branches of the Hymenoptera became fully social at least as early as the Cretaceous.

* The geological periods mentioned are arranged in the following order, from the present back: Pleistocene, Pliocene, Miocene, Oligocene, Eocene, Cretaceous, Jurassic, Triassic,

Even if we take Upper Cretaceous and Lower Pliocene as the two dates in question, social insects have been in existence well over five times as long as even the most primitive man; and the ratio, if we take the Triassic for the ants; and the Old Stone Age for man, becomes more like a hundred times.

This difference in evolutionary past has another aspect. We have just seen that the societies of ants have changed extremely little since the Oligocene, about thirty million years ago. But we all know that the societies of man have changed profoundly since man's origin, and, what is more, that the change shows no sign of abating into a stable phase, but has, rather, been progressively accelerated throughout man's history. This points the way to the last and most fundamental distinction of all, on which all the others hinge—the difference in the very structure of the societies and in the whole type of behaviour of the two kinds of organism. The insect imago, or adult, appears upon the scene full-grown, with a full complement of diverse instincts, and does not require any teaching to be able to carry out all the duties biologically required of her. True that she possesses a quite definite, if restricted, power of learning, but this enables her rather to adapt her instinctive behaviour to this or that detailed difference of the environment, not to ascend to wholly new levels of behaviour. Furthermore, the major part of the division of labour in an insect society is predetermined by the structure of body and brain. Usually the different castes are of different structural pattern. The smallest neuters of many legionary ants are several hundred times less bulky than the males or females, as well as being of quite different appearance, those of *Carebara* well over a thousand times; the head of the soldier of the harvesting ant *Pheidole* is bigger than all the rest of the animal put together, while in the worker it is of normal proportions. The worker bee not only has a larger brain than the queen, but has her legs

equipped by heredity with all the tools and gadgets needful for collecting and carrying pollen. Occasionally a division of labour is secured by means of a succession of different instincts in time. The young worker honey-bee helps tend the brood, but there comes a time when she abandons this and begins collecting nectar and pollen. This change of habit has nothing to do with learning, but depends on some development within the brain as definitely as does the change from tadpole into frog depend on material changes in the body.

On the other hand, by far the greater part of division of labour in human society is not predetermined through inborn structure, but is the result of learning. Even where a caste-system has been in operation for centuries, it has had negligible effects upon man's all-round capabilities. Man does not find his tools growing upon his body; he has to make them in infinite variety. His instincts are less specific than the insects', and are gradually overlaid by habit, experience and intelligent purpose until all trace of the original purely instinctive actions are supplanted by learnt behaviour, often of wholly new type, the instinct being merely the buried conduit along which the impulse to action must flow for part of its course. And finally man alone among animals has come to possess conceptual thought and a cumulative tradition. It is this cumulative tradition, based upon rapid learning and conceptual thinking, which has allowed human society to make such rapid evolutionary progress. What is more, the plasticity thus gained has made it possible for man to exploit all the regions of the globe, from Greenland to the tropical jungles, from the Sahara to the Alps, and to reap the advantages of the most varied modes of life, from miner to office clerk, fisherman to factory worker, while still remaining contained within the limits of a single biological species. The social insects achieve the same result, of exploiting

the most diverse geographical regions and ways of life, but they can only do so by quite other means. Since their achievement is based almost wholly on ready-made structure, whether the obvious structure of bodily tools, or the concealed but none the less real nerve-structure which is the physical basis of instinct, they can only adapt themselves to large changes of surroundings or way of life by means of alterations in their inherited construction. In other words, they must rely for their adaptations on mutations in their hereditary constitution, which is, of course, in the absence of further mutations, fixed and stable. Thus, while in man each new mode of life requires only a new habit and tradition flowering out of the old germ-plasm, in the insect it demands a new species with changed germ-plasm. The social insects thus exploit the world as a group of separate species, uncombinable biological units, man as a single biological unit, the separateness of whose minor groups is in the main transitory and preventable.

This difference is a particular case of a general principle of evolution. Wherever there exists specialized detailed adaptation, whether of bodily structure or behaviour, there we find groups with a great multiplicity of separate species; wherever structure or behaviour is either generalized or plastic, there we find fewer species in the group. This principle works both when specialized are contrasted with primitive groups, and when they are contrasted with progressive but plastic forms.

To take the contrast of specialized with primitive, there are many more species of bony than of gristly fish, of Pliocene mammals than of Eocene mammals, of insects than of Annelid worms. If we contrast less plastic with more plastic, there are many more birds than mammals, and this again in spite of the birds' greater mobility; more snails than cuttlefish and octopuses, more monkeys than apes. Finally, man, on account of

his almost unlimited plasticity, takes living matter on to a new level, where the most extensive adaptation can be achieved, and the whole group yet remain constituted by a single species. Man and the insects thus make the most complete contrast in this respect—the two most successful biological groups in existence, one consisting of nearly half a million kinds, the other but of one. And this consequence is in the long run a cause of the limitation of progress in the less plastic, of further progress in the more plastic.

There is every reason for believing that ants have long since reached the highest level possible to them, and equally every reason for believing that man is only at the bottom of his evolutionary ladder.

CHAPTER II

THE ANT STATE

THE ants are of all the social insects the most successful and perhaps the most extraordinary. All their more than 3,000 species are social, and show caste-differences, although their societies vary enormously both in size and complexity. Some species boast no more than a few dozen individuals to a nest, whereas in forms like *Atta* a single colony may muster half a million.

Ants (save a few monstrous queens, sluggish and bloated with eggs) never attain the individual size of some wasps and bees. Even the largest neuter ants fall far short of a gram in weight; in other words, it would take well over a hundred thousand of them to outweigh an average man. The range of adult ant-

size, however, is much greater than that of man. Even if we include dwarfs at one end and monstrosities of fat at the other, the largest human being weighs not more than twenty-five or thirty times as much as the smallest; while if we include normal specimens the figure will be reduced to under ten times. But the tiniest ants, like the smallest workers of *Carebara*, weigh several thousand times less than their largest relatives. Even in one and the same colony, individual bulk may vary up to a thousand times, as in *Carebara* again, or nearly to the same extent as if Lilliput were sober truth, and Lilliputians and normal men and women lived side by side in one community.

The dwellings of ants are usually underground, and are always characterized by great irregularity of construction as compared with those of bees or wasps. Gone are the honey cells, gone the separate room for each grub. What remains is an irregular series of chambers, connected with each other and the exterior by an equally irregular series of passages. Owing to this lack of geometrical precision, their constructions are less immediately interesting to us; none the less, their irregularity is really a sign of evolutionary advance, for it means that their habits are much more plastic and adaptable, and that, if conditions become unfavourable, the old nest can be abandoned and a new one constructed with a minimum of time and labour. The same is true of their care of their young. The young have no fixed and permanent cribs, but are carried from chamber to chamber as convenience and the conditions of moisture and temperature dictate; the pupæ may even be taken out for a sun-bath, and the whole brood may be rushed to a place of safety when the nest is disturbed.

This method obviously has direct advantages over the more mechanized procedure of the bees. It also has indirect advantages, in that it assures the workers

a much more permanent and intimate contact with their young; and this cannot fail to have reacted upon the evolution of their minds.

If this continued contact with their helpless charges has favoured the growth of many social qualities of their nurses, the intimate contact with their surroundings fixed upon them by their terrestrial habits must have favoured intelligence and pertinacity. As Espinas pointed out half a century ago, in regard to this very point, "on the earth there is not a contact that does not yield precise information." We may add that the obstacles to be constantly overcome (think what a formidable jungle is the grass to an ant dragging its prey, what an Amazon is every streamlet!) must provoke the development of perseverance in ingenuity. Further, "to employ matter is easier for a terrestrial than an aerial animal. The latter, when it is necessary to build, must, like the bee, either secrete the substance of its nest, or seek it at a distance, as does the bee when she collects propolis, or the wasp when she gathers material for her paper. The terrestrial animal has its building materials close at hand, and its architecture may be as varied as these materials." Ants, therefore, probably owe their "social and industrial superiority to their habitat."

It may be added that their dietary habits are equally plastic and varied, as we shall see in a later chapter. The bees confine themselves to nectar and pollen; the wasps live mainly upon other insects, with nectar and very rarely pollen as subsidiary foods; the termites are wholly vegetarians and mainly cellulose-eaters; but the ants eat not only insects and other animals alive or dead, but seeds, fungi, nectar, the honey-dew voided by plant-lice, and many substances which they find in the storehouses and kitchen cupboards of man. Some single ant species have been broken through the all-but-universal rule of food specialization among the insects and have become prodigies in their group by being practically omnivorous.

Most ant-nests, as we have said, are usually irregular and subterranean; but in most cases the excavated earth is thrown out above ground in the form of mounds, and these may be large and be tunnelled and chambered like the rest. Sometimes the main nest is above ground, like the familiar mounds of the big wood-ant of Europe, built of twigs and pine-needles, to three or four feet high. In the tropics and sub-tropics, however, a much greater range of constructional method obtains. Some ants make earth-nests high above ground by plastering earth round the branches of trees; others have reverted to the use of carton like the wasps, and suspend their tough papery dwellings from boughs; others inhabit natural cavities in trees or shrubs; and still others build nests of leaves.

Some of the cavity-dwellers live, not in accidental cracks or rotten holes, but in tubes or chambers which exist as part of the normal structure of certain plants. The fact has given rise to long controversy, some maintaining that the existence of these cavities is quite accidental, while others assert that this is a case of mutual advantage, the presence of the ants helping to protect the plant, and the cavities having thus been developed by natural selection to attract and retain the ants. The second supposition is rendered *a priori* probable by the constancy with which certain ants inhabit only certain cavity-producing trees, and also by the elaborateness of some of the cavities. But it cannot be said that proof has yet been obtained of the advantages supposed to accrue to the plant, so that the matter is still in suspense.

Some of the leaf-builders provide us with a very startling piece of behaviour. They employ child labour. Dofflein records how he deliberately made a small hole in such a nest. Almost immediately a number of workers ran up on the outside and, beginning where the rent was narrow, pulled its two edges together, holding on to one side with their jaws, to the other

with their feet, and so gradually approximating the edges throughout its length. Meanwhile another gang of workers had swarmed up on the inside. These were carrying larvæ in their jaws. When the outside gang had pulled the edges into position, those on the inside began squeezing their charges with their jaws. On this the larvæ started to secrete abundantly from their salivary glands. The secretion is strongly adhesive, and the workers use it to stick the edges of the tear together, passing the larvæ to and fro from one edge to the other like so many living shuttles. This same method is also used in the normal building of the nest. The differences between human and ant behaviour are beautifully illustrated by these ants. In so far as the ants adapt their weaving movements to the form of the rent, they are exercising a low but definite form of intelligence. But the basis of the whole action, the utilization of the larvæ, is instinctive. The whole structure of the larvæ is hereditarily altered in relation to their use as builders' tools. Not only are their salivary glands much larger than normal, but their saliva is unique in its stickiness. Without these genetic alterations, which the ants are no more able to bring about than we have consciously brought about the presence of hydrochloric acid in our stomachs or the shape of our bones, the actions of the workers would be entirely useless in the building of the nest.

CHAPTER III

LIFE HISTORY

IN all but the few parasitic ants, which will be described later, the method of founding new colonies is essentially similar throughout the group.

Only the males and females are winged, and they leave the nest for the nuptial flight, usually in swarms of many males and many females from each nest. Any country dweller knows how sometimes the air will be filled for miles with the flying sexual forms of some common kind of ant. Usually these mass exoduses from the subterranean nest-chambers to the free air occur on still, sultry days; and there seems no doubt that particular weather conditions stimulate the males and queens to fly out, thus insuring that many nests shall discharge their reproductive units at the same time, and so promote cross-fertilization between nests.

Neither the short-lived males nor the long-lived queens use their wings save on this one occasion. Fertilization takes place in the air, and the queen, the hundreds of thousands of spermatozoa needed for the rest of her career now safely stored in the little bag, with the tight purse-strings of muscle round its neck, which opens out of her genital tract, descends to earth. There she casts her wings and either digs a little chamber in the soil or finds one ready made under stone or bark. This done, she closes the door of the cell and becomes a voluntary prisoner. Strange to say, the eggs in her ovaries are unripe and minute at the moment of her flight—perhaps in order to save weight and make flight easier—and must now take weeks or even months to ripen. What is more, these weeks or months must be spent without food.

It is the same problem which confronts the

migrating salmon, who does not feed in fresh water on his journey to the spawning-grounds; and it is solved in a somewhat similar but neater way. Large muscles are, of course, required for flying. The shedding of the wings influences these muscles in some specific but not understood way, so that they break down and their substance dissolves and is gradually passed into the blood. This, and the stored fat in her abdomen, constitute the queen's internal food-store. Nourished by this, she matures and lays her eggs, and then, when they hatch, feeds the grubs with her saliva. This food is, of course, not very abundant, and as a result the first workers to emerge are always abnormally small. They at once dig their way out, find food, and take charge of the second batch of young.

The rearing of the young is no light task. In the first place, the eggs appear incapable of hatching unless continually licked by the workers; they must also be carried from place to place according to the conditions of temperature and moisture within the nest. Similar treatment is accorded both to larvæ and pupæ, and seems to be necessary for pupal development—in striking contrast to the bees and wasps, where the eggs are never touched by the workers, and the insect never leaves its little cell until it emerges as a perfect imago. The young are entirely fed by the workers, either with cut-up insect-meat, or in all higher forms by liquid regurgitated from the crop. Strange to say, the larvæ void no fæces, and are, indeed, incapable of doing so, since their stomach does not open into their intestine. The communication is only established just before pupation, and then all the accumulated fæces of larval life are extruded as a single large pellet. This is, perhaps, an adaptation for making easier the task of the workers in keeping the nest clean.

The grubs are regularly washed by their nurses, but this licking, though undoubtedly conducive to cleanli-

ness, springs largely—as we shall see later—from greed on the worker's part. The full-grown grubs spin themselves cocoons, and in this guise are often mis-called "ants' eggs." Finally comes emergence to the unchanging adult state. Here ants once more illustrate the general rule that biological progress goes hand in hand with the greater dependence of the young; almost alone among insects, they require help, or at least are helped, out of their prisons. The adult neuters first help by biting holes in the cocoon; but the insect which then appears is still so far from independence as to merit the special name of a *callow*. It is not fully pigmented, and is still enclosed in what looks like a shirt, but is really its final moult. This is pulled off by the nurses. "When we see how gently this is done," says Büchner, "and how the young creature is then washed, brushed, and fed, we are involuntarily reminded of the nursing of human babies."

Lord Avebury made some interesting observations on the delegation of different tasks to different individual workers. This he did by making hourly observations every day for three months on a small artificial nest, in which the workers had been marked so as to be individually recognized. The colony was fed by being given honey at a definite spot outside the nest. The observations were made during the winter, when not much food is required. For over two months the honey was visited—with a few casual exceptions—by three workers only, which thus acted as sole foragers and transport workers and fed the rest of the colony by regurgitation. At the end of this time he imprisoned one of the three, and on the same evening another ant came out to the food. This new forager continued regularly at its task until after two days she also was imprisoned. Two days later a new forager appeared, joined a few days later by another. In another nest the same thing happened; but here

none of the original foragers were imprisoned, and accordingly continued without change for the three months of the experiment.

How this division of labour is determined is not clear. The beautiful studies of von Frisch on bees, based on the same methods of individual marking, patient observation, and experimentation employed by Lord Avebury, have revolutionized our ideas of bee life. It is certain that an equally rich harvest of knowledge and interest awaits anyone—for the work can be carried out by an amateur just as well as by a professional biologist—who is willing to devote himself to a full study of marked ants, and thus to record the history of a single colony from the start.

It may take several years before a colony is adult; and, even when the swarms of new males and females are discharged, the old colony will continue. For one thing, the old queen may live ten years or more—seventeen-year-olds have been recorded—and will continue—still by means of her single original store of spermatozoa—to produce fertilized eggs until her death. Then, too, in many ants, some of the daughter queens regularly return to the nest after being fecundated, and, since the queen ant, unlike the queen bee, is never hostile to other queens of her own species, the nest comes to have a multiplicity of egg-laying queens, and so becomes potentially as immortal as a human nation. If such a colony continues to grow it will reach an inconvenient size, its food-needs outrunning its communications. When this happens new nests may be formed, just as new settlements were formed by the Greek cities, a band of workers with one or more queens leaving the old home to found a new one. Sometimes the new home is not far from the old, and then a federation of colonies is formed, differing from a number of separate colonies in the fact that all the workers are on friendly terms, and may pay visits to other nests within the federation.

When a solitary queen founds a separate colony, on the other hand, the workers of this colony will exhibit hostility to those of all other colonies of the same species, including that which gave birth to their own royal founder. It seems probable that the friendliness or hostility of the workers to other ants of their own species depends on smell, each nest having some subtle "nest-smell" which is caused by each of its inmates. This smell-based friendliness may be extended to ants of other species, and even to other insects. Not only must the mixed colonies of the slave-makers and the parasitic ants (Chapter VII.) obviously be based on this acquired tolerance, but mixed ant-colonies may be artificially built up by human agency. Miss Fielde, following up some work of Forel, gave to one species of ant the pupæ belonging to another species of ant. When the alien workers hatched out they were accepted as part of the colony. Not only this, but they later showed marked hostility to their own blood-sisters who had been left to grow up in their own nest. Smell is thus to the ant what national traditions are to us—the basis of patriotism; and this patriotism, again as with us, can override the ties of blood and force relatives to fight against each other. In both cases the same end is secured—the subordination of the individual unit to the social unit of which he happens to form part: but the means are different.

The mixed colonies which are to be found in Nature always consist of two quite closely related species. This is, in the main, due to the fact that the rearing of the young is a complex and delicately adjusted process, so that the needs of the larvæ of one kind of ant could scarcely be met by the instincts of the workers of some very different species. When, however, this difficulty is eliminated, as in Miss Fielde's experiments, by inserting full-grown larvæ into a strange nest, it is observed that smell covers a multitude of differences, for she could thus found

compound nests even with two species of widely separated sub-families. The nest-smell doubtless also envelops in its protective mantle most of the many ant-guests, other kinds of insects which live dependently in the abodes of ants; but this we will consider later.

As regards caste and sex, all ant-species possess at least one sterile caste, the workers, in addition to fertile males and females. Anatomy reveals that the worker is a sterilized or neuter female, in whom may be distinguished rudimentary ovaries and oviducts. It seems certain that the difference between female—whether fertile queen or sterile worker—and male is determined, as in bees and wasps, by fertilization or the lack of it. Fertilized eggs produce females, unfertilized eggs produce males; and the control of sex-determination is exercised by means of the tight sphincter of muscle which in the queen's body surrounds the orifice of her purseful of sperms. If this is opened as an egg passes over the aperture, one or a few sperms pass out, and fertilization occurs; if it is kept shut, the egg remains unfertilized and male-producing. We know very little of what influences the queen ant to open or close this destiny-determining circlet of muscle. The differences between neuter and queen appear, again as in most other social insects, to be determined by differences in the quality of food given to the young larvæ, but here once more we know more of detail in bees than in ants. What causes the difference between winged and wingless queens or males, when both forms exist, is not yet known.

The fact that the differences between male and female are determined by heredity, those between queen and neuter by subsequent treatment, is shown by a study of the occasional mosaic monstrosities which occur when one-half or smaller area of the body is of one type, the rest of another type. Now, combinations are known of male part with queen part, of male with

worker, and of male with soldier; but never of queen with either worker or soldier. All such monsters (called *gynandromorphs*) are to be explained through some abnormality of fertilization, presumably through the sperm entering only after the egg has begun to divide, and uniting with the nucleus of one only of the two or more cells produced.

Ants which partake of the nature of both queens and neuters do occur; these, however, the so-called pseudogynes, are never mosaics, but intermediate in every part. They seem to be the result of an alteration of diet in the middle of the grub's development. These pseudogynes, and also occasionally true workers, may lay eggs; but, as the animals have never been fecundated, the eggs can only produce males.

CHAPTER IV

FOOD-ECONOMICS

THE members of a human civilized community are tied together by economic bonds. Nobody but the cultivators of the soil can feed themselves by their own labour, and even they tend to specialize on one product, acquiring the rest of what they need by way of exchange. The agricultural population of Java, for instance, is so dense that it can only be kept alive by the import of rice, which is paid for out of the surplus of the exports of the more valuable coffee, rubber, and other vegetables which they cultivate.

With us, of course, there is a universal medium of exchange in the shape of money, and by the use of such a medium we raise our system of mutual ex-

change of services to a far greater level of flexibility than was possible by means of payment in kind or direct barter. The ants in an ant-colony are equally tied into a single economic whole; but the means by which this is accomplished are as unlike and, indeed, alien to those employed by man as is nest-smell to our methods of securing patriotism and the social subordination of the individual.

In the first place, the whole of the colony have, for practical purposes, but a single stomach. This arrangement occurs in such creatures as colonial polyps; but in them it is ensured by direct and permanent communication, the digestive cavities of each individual opening into a common communicating tube in the stalk. The ants have perforce had to adopt a less simple method. The food, after it has been reduced to a liquid soup, is passed down the narrow gullet, which pierces the nerve-collar in the head and traverses the whole thorax to open into the crop (or, as Forel, for reasons soon to appear, christened it, the "social stomach") in the fore part of the abdomen. The crop opens by a complicated valve into the true stomach, which in turn leads into the small intestine, and so *via* the large rectum to the anus.

When a worker has had a good meal, only a fraction of the partially digested food stored in the crop reaches the stomach and intestines, and is absorbed by the animal itself; most of it is distributed to other members of the colony, who solicit it by protruding their tongues and stroking the fortunate one with rapidly vibrating antennæ. On this, a drop of the food is regurgitated from the crop and passed into the other's mouth. The proof of the pudding is in the regurgitation. If an ant be allowed to gorge itself on syrup stained, say, blue, with an aniline dye, the colour will show bright through her abdomen, and, as she distributes portions of it here and there among her fellow-citizens, and they repeat the process, the

abdomens of almost every individual will become faintly tinged with blue. The collective stomach of the colony has been fed.

The food-interrelations between workers and larvæ are even more remarkable. The larvæ recapitulate a less specialized past in having a simpler gut, without a "social stomach," and in being able to deal with solid as well as liquid food. Many of them have a number of spines and roughened ridges near the base of their jaws. These when rubbed against one another possibly generate shrill sounds which, like a baby's howling, may serve to attract their nurses' attention. The remarkable facts elicited notably by Roubaud and by Wheeler both in ants and wasps show that the grubs, after being fed, secrete some liquid which the workers eagerly devour. In wasps and many ants this liquid is a specially sweetened saliva; but the majority of ants exude a fatty substance through their cuticle. In one sub-family of ants the larvæ are provided with extraordinary appendages which secrete a substance of this kind in more concentrated form, and are, one presumes, easier to suck.

To quote Wheeler's words: "Although these various substances are produced in very small quantities, they are of such qualities that they are eagerly sought by the adult ants. This explains much of the behaviour which has been attributed to maternal affection on the part of the queen and the workers, such as the continual licking or fondling of the larvæ, the ferocity with which they are defended, and the solicitude with which they are removed when the nest is disturbed. In other words, a decidedly egoistic appetite and not a purely altruistic anxiety for the welfare of the young constitutes the potent 'drive' that initiates and sustains the intimate relations of the adult ants to the larvæ, just as the mutual regurgitation of food initiates and sustains similar relations among the adult workers themselves." This payment

by the larvæ for services rendered, Wheeler has christened *trophallaxis*, or exchange of food-stuffs. Thus, if the ants' patriotism is based on smell, their economic and social stability is founded on taste. The two cementing principles are rather different, since the common smell merely envelops the colony and binds it together, whereas in trophallaxis there is a real economic exchange and a true bargain struck, the larvæ presenting the adults with coveted substances, unobtainable elsewhere, in return for attendance and plenty of plain food.

Since the subject is of such vital importance, we may here diverge a moment to look at trophallaxis among the wasps, where it exhibits certain simpler and more clear cut features. The substance offered by wasp grubs to their adults is always the secretion of the salivary glands, which have apparently lost all their digestive functions and now secrete an abundant sugary liquid entirely devoted to rewarding their nurses.

Roubaud describes the act of trophallaxis thus: "As soon as a nurse wasp has distributed her food-pellet, she advances with rapidly vibrating wings to the opening of each cell containing a larva in order to imbibe the saliva that flows abundantly from its mouth. . . . The wing vibrations of the nurse serve as a signal to the larva which, in order to receive the food, protrudes its head from the cell. This simple movement is often accompanied by an immediate flow of saliva. But if the secretion does not appear, the wasp seizes the larva's head in her jaws, draws it towards her, and then suddenly jams it back into the cell, into which she then thrusts her head. These movements involve the stimulation of the larva's mouth, and force it to secrete its salivary liquid."

The nurses may return three or four times to obtain this secretion after they have fed their charges but once. What is more, the larvæ are sometimes ex-

plotted, and, by means of the curious handling just described (which appears to be instinctive, in origin at least, on the part of the adults), made to secrete saliva without any compensatory gift of food. This, which amounts in the wasp's economic system to thieving, is practised almost entirely by workers which have just emerged, by the queen, and by males. It is interesting to find that this secretion can be artificially induced, either by touching the larvæ on the borders of their mouths, or by simulating the effect of the nurses' vibrated wings by whistling near by. "It is only necessary to whistle loudly or emit shrill sounds near a nest of *Belonogaster* to see all the larvæ protrude their heads at the orifice of their cells."

J. B. S. Haldane has pointed out a further biological meaning in the wasps' trophallaxis. Most of the food actually in the blood-stream of a mammal is utilized as fuel, in the form of sugar. The nitrogen-containing amino-acids derived from meat and other proteins are employed for tissue repair, but only quite small quantities are needed for this, the remainder being broken down into sugar further utilizable as fuel and waste nitrogenous substances like urea. The growing puppy or human child, on the other hand, utilizes a much greater amount of its nitrogenous food, since it has to build tissue as well as repair it. In these respects, insects are like mammals, but more so, since the cold-blooded, sluggish grub requires relatively less fuel. Thus trophallaxis as practised by wasps is not only a system of services and rewards—it also ensures a more economical utilization of the food. As Haldane says, "When a worker comes to feed a grub . . . the grub thanks it by secreting a drop of fluid containing sugar for which it has no use, but which is valuable fuel for an active insect" (and one, we may add, which is no longer growing).

The bees, curiously enough, appear to lack all trophallaxis between grub and adult, nor is there any

transference of food from one worker to another. The first point may be accounted for by the facts mentioned by Haldane. The food of bees consists mainly of the sugar-containing nectar, transformed into honey during its sojourn in their crop, and the pollen, or bee bread, rich in protein. The adult bees require no extra carbohydrate, since they obtain it directly in their ordinary food; the grub can have its nitrogenous and non-nitrogenous rations exactly dosed. The lack of mutual feeding by the adults can be equally easily accounted for: the bees have produced an artificial substitute for the "communal stomach" of the ant colony, in the shape of their cells of pollen and honey. The workers regurgitate their gathered stores into these instead of into other workers' mouths; and, since some of them are always left open, home-staying bees can always draw upon them when hungry.

Finally, the Termites have developed very extraordinary systems of communal food exchange, which will be discussed in a later chapter.

CHAPTER V

ANT SENSES

THE senses of ants are of considerable interest. Sight can never be very acute, as the compound eyes have few and widely diverging facets. The simple eyes or ocelli, present in almost all forms, can only serve for extremely near vision, or perhaps merely for distinguishing light from darkness. The Driver ants, for all their ferocity and active migrations, are wholly blind. It is of some interest that some ants, at least, are sensitive to a certain range of ultra-violet light unperceived by us.

In ants the only sense organs of any delicacy of discrimination are the antennæ. These mobile organs explore the environment with a combination of smell and of touch in a way which we, with our organs of smell fixed within our skulls, can scarcely imagine. Smells for us are without form and void. But ants can undoubtedly distinguish the shape of all such smells as are being given off by definite bodies of small size, and they must have a composite notion of such a body in terms of colour, flat shape, and shading derived from sight, and solidity derived from touch. In the battles between different colonies of the same species of ant, friends cannot be distinguished from foes by distinctive markings or uniform, nor are there any battle-cries. It appears that a touch of the antennæ at once decides the point.

An obvious problem of ant biology is to know how they find their way back to the nest after long expeditions into the surrounding country. Once well-marked trails have been established, the track itself and the smell adhering to it simplify matters a good deal. But what of solitary workers exploring off the beaten track, and their power not only of returning to the nest, but also of bringing back a band of other workers to any source of food they may have discovered?

As a matter of fact, most species of ant seem to employ three or four different methods in finding their way. To a slight extent they utilize what to us is the most important method—that of orientating themselves with regard to objects in the landscape. Wherever there exists a trail over which they or other ants have gone, they rely largely upon smell. Smell, however, cannot very well tell them much about direction. Although Bethe put forward an elaborate theory in which he supposed that an ant, by means of its power of detecting the shape of smells, could distinguish in which direction ant footprints were headed, he had to make the further supposition that the ants

travelling out from the nest imparted a somewhat different smell to their traces from those coming back. Recent workers, however, following up a clue left by Lord Avebury, have been able to show that this is not so, and that the ants are guided in their direction by the direction of the light falling upon them. If, for instance, a solitary questing ant is imprisoned under a box for three hours, and the box then taken off, it sets off in a direction which deviates from its original line by the same angle through which the sun has travelled during its imprisonment—in this case 45 degrees. This it will do whether it had been travelling directly towards or away from the sun, or at an angle to its light. In artificial nests the ants can be completely tricked by moving the source of light. Apparently, on days which are overcast, the ants can still orient themselves approximately in relation to the part of the sky most strongly illuminated; but more experiments are needed on this point.

Finally, the ants must have some sort of sense of distance, for when an ant has been tricked, by being kept prisoner for a time, into following a false direction on its homeward way, it stops its straight, unhesitating march when it has travelled a distance, which, had it been moving straight homewards, would have brought it to the near neighbourhood of the nest, and begins to quest about in every direction. Apparently this faculty depends on some utilization of the kinæsthetic or muscular sense, the number of leg-movements being more or less accurately registered. It is certain that a similar mechanism is at the basis of the power of rats and other animals to learn a maze. Whatever the precise machinery at work, there is no doubt that many animals do possess some such automatically registering pedometer as part of their equipment.

Many are the stories of ant intelligence. Most of them, however, smack much rather of trial and error,

or of adapting instinct slightly to unusual circumstances, than to intelligence properly so called.

Some ants are undoubtedly very stupid, judged by our standards. Lord Avebury found that the little ants which he kept in captivity could not learn to build up earth into a pile an eighth of an inch in height in order to get at some honey which they could smell and see just out of reach, nor to perform a number of equally simple mechanical acts which would have secured them food or access to their larvæ.

On the other hand, there are trustworthy accounts of Driver ants bridging streams by each worker seizing a twig and then forming a living chain-bridge across the water, over which the rest of the army can cross; and Bates himself records how the path of some South American ants lay across a tram-line, and how, after a large number had been squashed by the tram, they made tunnels under the rails. When Bates stopped up these tunnels the workers refused to cross the rails, but waited until new tunnels were made. Cardinal Fleury communicated to the great Réaumur his observations of how ants surmounted a girdle of bird-lime smeared round the trunk of a tree by laying a road of earth and small stones across it; and the fact has been corroborated in recent years, one observer stating that he had seen ants, trapped on a tree by a band of tar, bridge the obstacle with their own ant-cows! Others in similar predicament have been known to reascend the tree and drop from the branches, although Lord Avebury's ants (perhaps because they belonged to a species with very poor sight and less roving habit) refused to let themselves drop through half an inch.

Some of the building activities of ants, too, display definite intelligence in the sense of the adapting of means to ends, but there, too, instinctive foundation always remains and is larger than the superstructure of intelligence. The enormous gulf between the intelli-

gence of ants and our own is most readily realized by reflecting that no ant receives any education. The larvæ are mere machines for growing up as quickly as possible, with the most rudimentary sense-organs and no limbs; even if they were taught, which they are not, their capacity for profiting from the instruction could not very well transcend that of an earthworm.

The pupæ are shut away from the world in their cocoons, busy with the task of transforming their whole organization from that of helpless gryb to winged six-legged creature. Finally the adults, once emerged, can set about performing all their complex tasks without the least instruction, as is shown both by observation of young nests and by experiment. They find the food proper to the species, they build the right kind of nests, they tend the young in one particular way. They may improve as the result of practice, or may have new habits thrust upon them by necessity and experience; but there appears to be no way in which tradition can be communicated from older to younger workers, and certainly no way in which it can be transmitted to a new nest. In respect of education and tradition, even the highest of social insects is below the level of a mammal like the dog.

All ants are extremely cleanly animals. Not only, however, are they cleanly with regard to their own persons, but their social nature prompts them to mutual assistance in matters of the toilet. We may take McCook's account of the operation in the fungus-gardener *Atta*: "We take a couple; the cleaner has begun at the face, which is licked thoroughly, even the mandibles being cared for. . . . From the face the cleaner passes to the thorax, thence to the haunch, and so along the first leg, along the second and third in the same manner, around to the abdomen, and thence up the other side of the ant to the head. . . . The attitude of the cleansed all this while is one of intense satisfaction, quite resembling that of a family

dog when one is scratching the back of his neck. The insect stretches out her limbs, and as her friend takes them successively into hand, yields them limp and supple to her manipulation; she rolls gently over upon her side . . . and with all her limbs relaxed presents a perfect picture of muscular surrender. . . . I have seen an ant kneel down before another and thrust forward the head, drooping, quite under the face, and lie there motionless, thus expressing . . . her desire to be cleansed. I at once understood the gesture, and so did the supplicated ant, for she immediately went to work."

Ants, like other higher insects at least, require sleep. The exposition of sleep may come on at any time of day, and its duration, in those species where it has been timed, averages some three hours. They may choose a depression in the soil as bed, and there lay themselves down, with legs drawn close to the body. When asleep, they may be stroked or tickled without awaking, though a sharper tap rouses them at once. When waking naturally, they behave in a way startlingly like that of mammals or our proud human selves. The head and then the six legs are stretched to their fullest extent, and then often shaken; the jaws are strained open in a way remarkably reminiscent of a yawn. One interesting observation made by McCook on an American harvesting ant with great difference in size between the workers and soldiers, was that the soldiers sleep longer, and also more heavily, being much less easily awakened.

Some observations indicate that ants have reached that high stage of mental development at which play appears. The sport generally consists in mock fight between the workers of a single colony, the ants behaving just like dogs when they play at fighting. They may also pursue each other, again like puppies, or like children playing tag.

This brief account of some of the general habits

of ants may fittingly conclude with a reference to the way in which their bodies are disposed of by the community after death. Some of the older naturalists gave the most circumstantial accounts of regular ant funerals, with corpses borne by workers two and two in procession, and finally interred in separate graves. It appears that imagination had here a little outrun fact; none the less, the fact is interesting enough. Most ants are extremely anxious to dispose of any corpses, and if kept in a small artificial nest will wander round with their burdens, often for days, searching for a suitable spot. In nature, the usual cemetery is simply the communal refuse-heap, so that it is probable that the corpses are merely regarded as so much refuse, and the apparent solemn burial of the dead turns out to be only a special case of the ants' passion, doubtless implanted by natural selection on account of its utility to the colony, for keeping the nest tidy. It has, however, been asserted that the slave-making *Formica sanguinea* has separate places of disposal for the corpses of its own species and that of its slaves.

CHAPTER VI

WAYS OF LIFE AMONG ANTS

ANTS are essentially terrestrial creatures, though a few have secondarily taken to tree-life. Though of world-wide distribution, they are pre-eminently inhabitants of dry or desert regions. In structure, they bear witness to definite relationship with the Scolioids, a group of solitary wasps, and there can be little doubt that

they have originated from a ground-nesting wasp of this type which took to social life with loss of wings in the workers, but not in the sexual forms. Their abundance in arid lands suggests that this development first took place in one of the long arid periods of the northern hemisphere, presumably in the Trias or Lias of the Secondary epoch.

At the beginning, all the workers were doubtless alike, and not markedly dissimilar from the queens. But terrestrial life and social specialization gradually rendered the ant neuter more unlike the queen than in any wasp or bee. Meanwhile, the average size of the colony doubtless increased.

There exist to-day seven sub-families of ants. Of these the Ponerines are undoubtedly the most primitive. In them and two other rather primitive sub-families the neuter is still almost as big as the queen, and there is never more than one kind of worker. Among the remaining four the neuters are often (though by no means always) divided into sub-castes, which differ not only in size but also in form, the larger always having relatively enormous heads and jaws. These big fellows are the soldiers, and usually live up to their name by acting as defenders of the colony, though in some species they help the larder by crushing up hard seeds or insects, which would defeat the weaker jaws and smaller size of the ordinary worker. Primitively it appears that a whole graded series of neuter types is produced. Later the middle forms (and sometimes also some of the smallest) may be eliminated, leaving only sharply defined worker and soldier sub-castes; or all the large and middle-sized types may disappear, leaving only the tiniest workers to carry on the business of the nest.

In addition, both queen and male castes may become sub-divided, wingless as well as winged forms being produced. And here again, in further evolution,

the original winged type may be suppressed, leaving only the wingless as reproducer-caste.

The two highest sub-families are the Myrmicines and the Formicines. Scarcely any other ants have succeeded in pushing out of the tropics or sub-tropics, but these groups are found abundantly over the north temperate region.

In the primitive sub-families the diet consists exclusively of other animals, mostly insects; thus ants as well as man began as hunters. One of these groups, the Dorylines, better known as Driver or Legionary ants, have raised hunting to a high pitch. They have no fixed nest, but range the country in huge bands, often of several hundred thousand workers, all blind, and all ferocious, devouring any living creature which does not take to flight, and many are the nests of other ants which fall a prey to them.

Among the higher forms many genera have left the hunting for the pastoral life, living directly or indirectly on the sap of plants. In some few cases this "honey-dew" is secreted by the plant in special nectaries on stalk or leaf, its function apparently being to attract ants, which then serve instead of thorns or bitter juice to help keep away devourers. But in most cases the ants take advantage of the much more abundant supply afforded by the various little sap-sucking insects—aphids, scale-insects, leaf-hoppers, and the rest. These wasteful creatures only use a fraction of the sugary solution which, with their sharp proboscis, they are imbibing all day long; the remainder exudes at their anus. The ants, however, always the exemplars of frugality, have not tolerated this waste. They either lick up the excreted "honey-dew" from the surface of the leaves, or "milk" the animals by stroking them with their antennæ. Finally, some species actually domesticate these ant-cows; and others store the honey-dew against the dry season—in an extraordinary way of which an account will be given later.

Then in some Myrmicines, the pastoral stage has given place to the agricultural. A halfway house is reached by the so-called harvesters, which collect the seeds of grasses and store them in regular granaries, although, contrary to early belief, they never sow seeds for a new crop, and so do not fully merit the name of agriculturists. But some other genera of the same sub-family practise a real horticulture, growing fungi for food, and attending to the growth and reproduction of their vegetable plots as assiduously as any human gardener.

Finally, as a strange overshooting of the mark, a specialization which eventually leads downhill, there are the thieving, slave-making, and parasitic ants. There exist ants which are occasional brigands; others which are persistent thieves, and some which are servile parasites. In both Formicines and Myrmicines, the subtler form of parasitism which starts as slave-making has been evolved. Some are temporary slave-makers, others must live with slaves all their lives, and still others have completely lost their worker caste, the queens and males living as mere parasites on their slaves.

There is no reason whatever to suppose that the ant-type will not continue to flourish through future geological periods as admirably as it has done in the past. As a type, it most efficiently fills a definite niche in terrestrial life. A few species will doubtless be exterminated by man, some deliberately, others as the unforeseen result of agriculture and other human activities; but the type as a whole will be protected by its small size, subterranean habits, and adaptability. New species and new modes of life will doubtless come into existence, but the type itself will persist essentially unchanged, as a witness to the biological success of social life utilizing the efficient machinery of insect structure and held together by firm and elaborate instincts.

After this brief general sketch of ant evolution, we

may turn to some actual pictures of ant-life, as led by different species of this strangest of all earth's little peoples.

MARKET GARDENING ANTS

Let us look first at *Atta*, chief among ant-gardeners. In the woods of Southern Texas there may occasionally be seen processions of ants, following well-worn trails often a hundred yards or more in length. Those going in one direction are empty-jawed, and walk on one side of the road; those going the other way keep to the other side and carry a piece of green leaf. The piece of leaf is often so large as to hide the animal that carries it, and has led to these creatures being called parasol ants. The leafless workers are on their way up trees; there they cut out their green "parasols" with their jaws; and thence carry them back to the nest, or let them fall one after another to the ground to be picked up by another gang there. The nest may be enormous, a veritable subterranean city, the débris of its excavations piled into mounds ten or twenty feet across. The mound of the common Brazilian parasol ant, *Atta sexdens*, may run to 265 cubic metres of earth, weighing many hundred tons, and may shelter over half a million individuals.

The neuters of *Atta* cover a great range of size, from the huge-headed soldiers down through large and medium and small workers to the tiny *minimæ*. The soldiers defend the nest, and police the bands of medium and large workers who make it their business to clip the leaves.

In the nest the leaf pieces are cut into smaller bits and built up into beds on the floor of the large subterranean chambers which other workers have previously excavated. These beds are then handed over to the smallest workers, who work only underground, though they are said to come up occasionally to play

about in the light and air. On the beds of decaying leaf a white network of fungus grows: this is tended by the smallest workers, who treat it by some unknown method which makes the threads produce clusters of small spherical swellings. These miniature white cabbage-heads are bitten off and used by the ants as the staple food both of themselves and their young. The ants seem very careful about the proper ventilation of the gardens, and Bates describes them as opening or closing some of the numerous holes leading to the surface from the fungus-chambers, according to the conditions of moisture and temperature. They are also careful not to bring in pieces of leaf if they are too wet, but leave them near the entrance to dry. Grass is apparently unsuitable for fungus-beds. In spite of this, ants are occasionally seen carrying bits of grass into the nest; but these are always thrown out again after a time.

Every species of *Atta* grows a different kind of fungus, and, what is more, weeds out any other which may start to grow in the nest. The fungus-heads are artificial productions of the ants' gardening just as definitely as are good white asparagus stalks the product of the treatment the plant receives from man: they do not appear when the fungus is grown in the laboratory. Indeed, they are much more modified than asparagus, for the fungus-threads are really the mycelium, or "spawn," of a regular mushroom. So long as the ants' cultivation continues, the fruiting mushroom structure never appears, but in abandoned nests they are sometimes found pushing up. Several distinct genera of fungus have thus been domesticated by the Atticine ants, including one which is not related to the mushrooms at all, but is more like yeast.

It is probable that the *Atta* workers manure the gardens with their own excrement. Certainly some related forms use the dung of caterpillars and other insects as the substratum for the fungus, in place of

leaves. Others suspend the fungus-beds from the ceiling.

The transference of the precious fungus from colony to colony is effected by the queens. All ants possess in the forepart of their mouths a pouch, the so-called infra-buccal pocket. Into this, in the ordinary ant, are swept first the more solid food-particles after they have been masticated by the jaws, and also, strangely enough, the combings and scrapings of the ants' toilet. These latter are combed off her legs and antennæ by means of a pair of opposable combs on the fore-leg, and licked off the rest of her body by the cleanly creature's tongue. The pellet in the pouch is moistened with saliva, which dissolves out any available food, and when it has reached a certain size it is thrown out. No adult ant thus swallows anything but liquids.

The pocket is utilized by the parasol ants for the inoculation of new nests with fungus. The virgin queen, before leaving the nest on her nuptial flight, takes a hearty meal—of fungus, of course. Threads of the mycelium, together apparently with some of the leaf-soil, are packed into her infra-buccal pocket. After she has mated, cast her wings, and constructed a small underground room as beginning of the future nest, she spits out the pellet on to the floor. The fungus, of course, begins to grow, and the queen tends it with the greatest care, manuring it with her feces, and even breaking up some of her own eggs to furnish more "soil." She uses the garden as a nest for other eggs; the larvæ from these hatch out, feed on the fungus, and turn into workers. These, untaught, break out of the chamber, raid trees for leaves, and take the charge of the garden off the queen's shoulders. Thus an extremely slight modification of an old-established habit suffices to ensure what at first sight seems to us no simple task—the transmission of the fungus-vegetable to new nests.

It is interesting to find that the cast pellets of most sorts of ants almost always contain fungus-spores. What is more, most ants have a regular refuse-heap in or near the nest, and many species make a practice of voiding their pellets here, just as man and several mammals, like the rhinoceros, prefer to defæcate in definite spots. This refuse-heap affords favourable conditions for the germination of fungi, and in point of fact in some species of *Crematogaster* not only does an abundant crop of fungus-threads grow on the refuse-heaps, but the ants actually use this as part of their diet. And from an accidental state of affairs such as this it is not a very large step to that found in the true fungus-growers. Thus even such a surprising activity as deliberate vegetable-gardening can have had a comparatively simple and intelligible evolution.

HARVESTING ANTS.

It was *Messor barbarus*, one of the harvesting ants to which Solomon referred when he wrote his celebrated advice to the sluggard (Prov. vi. 6). It was for many years believed that these creatures not only stored grain but actually sowed it in definite fields in order to raise a new crop. In view of what has occurred with the fungus-growers, this would be quite possible (save that it is more difficult to think of the practice arising when months instead of days or hours must elapse before the new crop appears); it merely happens not to be true. These ants often clear a considerable area round their nests; and on this bare area grasses may sometimes be found sprouting. However, this is not due to any deliberate sowing by the ants, but only to the germination of accidentally dropped seeds.

The harvesters are all inhabitants of desert or semi-desert regions. Not only is insect-food scarce, but

there are long periods of drought in which both active plant and animal life is almost absent. Thus the ants find in seeds a welcome addition to their diet, and also a food which can be stored against a dry season. When they can find insects, they still will eat them readily enough. Several of these ants have neuters ranging from small workers up to huge-headed "soldiers." These latter, although they are precisely similar in general structure to ordinary soldiers, have taken upon themselves a new and different function. The larger and harder seeds are broken up by them with their enormous mandibles, and so made available to the rest of the colony.

In some cases—for instance, the Myrmicine harvester (*Pheidole instabilis*) from Texas—there is a complete and continuous gradation between the largest soldier and the smallest worker, as in *Atta* and some of the Driver ants. When the whole series is examined it is seen that the differences between the various forms are differences of proportion: the larger the neuter, the relatively larger head-organs does it possess. What is more, whenever in such forms the weights of head and body are taken, it is found that they obey a simple mathematical relationship—head-weight is a function of rest-of-body weight raised to a power; and this would imply that head and body grow at different rates, but rates which always bear a constant ratio to one another, like two sums of money accumulating at different rates of compound interest.

These facts give us a probable clue to the origin of the sub-castes among ant neuters. There is always some variation in the adult size of insects, due to the quantity of food available to the larvæ. The social insects are no exception to the rule; one of the most striking examples is given by the Humble-bee, in which the first-hatched members of a new nest, owing to the overworked queen not being able to provide a great deal of food, are always smaller than their

mother—sometimes scarcely larger than house-flies—although they are not neuter. The neuters of all ants vary in the same way, the range of size being much greater in some species than in others. In many cases the difference is one of size alone, the proportions of parts remaining the same. Even here the variation may be turned to advantage, very small workers being suited for delicate work in the nest, very large ones for heavy jobs in transport or construction; and, if advantageous, the condition would readily be brought about through the nurses giving abundant food to some larvæ, very little to others.

But growth of all parts of the body at the same rate is really only a special case; in reality, different parts usually grow at slightly different rates. The jaws of ants are their main tools and weapons both. Thus the advantages of size-variation would obviously be intensified if the large individuals had also more powerful jaws—and therefore, because of the muscles required, larger heads—and this would be insured if in the pupa the rate of growth of the rudiments of the adult head was greater than that of the rest of the body. Not much difference is necessary; the head's growth-rate need never be twice as great as the body's to produce soldiers which are almost monstrous.

Thus the whole gamut from super-soldier to *minima* workers one-fiftieth their bulk could be produced by a combination of two well-known principles—variation in imago-size dependent upon the amount of food received by the larva, and the differential growth-rate of one region of the body. The growth-rates are given by heredity; once they are established, all that is needful is that the worker-nurses should vary the food-supply of the grubs. The view that this has actually been the course of events in ants is supported by the fact that whenever new nests, of species with polymorphic neuters, are founded by single queens, the first brood consists only of small workers and never contains

soldiers; for the same reason, one presumes, that the first brood of humble-bees are small—because the queen has not time nor energy to feed them up.

In the genus *Pheidole*, some species, like *instabilis*, exhibit the complete gradation we have just studied; but the great majority possess nothing but soldiers and tiny workers. This must be due to a further specialization of the nurses' behaviour—they either feed their charges to the fullest extent, or keep them on a definite scale of reduced rations. The result is a sharpening of the division of labour—a specialization perfectly analogous to that between the different tissues of the body.

ANT-COWS.

It was Linnæus who first christened plant-lice the ants' cows; and the phrase is perfectly legitimate. The domestication of plant-lice has reached such a pitch among certain ants that the masters—or, rather, mistresses—collect the "cows'" eggs in autumn, keep them through the winter in their own nests, tending them like their own, and in the spring, when they begin to hatch, plant them out in their pastures, distributing them over the roots, leaves, or stems of neighbouring plants. For instance, *Lasius americanus*, one of the commonest ants of the United States, distributes plant-lice far and wide over the roots of Indian corn; while in the European *Lasius flavus* Lubbock found them planting out eggs on to daisy-plants, and others take their charges high up on to trees. Other ants keep their dairy beasts browsing on roots in specially constructed rooms underground, or even build sheds or barns over them as they suck the juices of leaves high up on shrubs or trees. These sheds are sometimes connected by long, covered ways with the nest. Care is usually taken to have the doors too small for the cows to get out, though big enough for the ants.

All such herd-masters practise the "milking" of their insects, stimulating them to defæcate by stroking their bodies with their antennæ. Darwin and others have tried to imitate this by stroking aphids with a hair, but this is of no effect; yet even very young aphids respond at once to the blandishment of the ants' feelers, though, in the absence of this stimulus, they hold up their secretion for long hours.

When the ant-cows are kept permanently underground, as in plant-lice and mealy-bugs tended by *Lasius americanus*, they become snow-white—not, as with our white cows or horses, through positive selection, but through the direct or indirect effect of the lack of light. What is more, their herd-mistresses, never needing to come above ground for their food, are pale yellow in colour, and have become almost blind, with vestigially minute eyes.

As we have seen, this dairying life has grown up naturally enough. It is based on the fact that the sap-sucking insects utilize only a small portion of the sap they pump up from the plant tissues, but void the major part of it. From licking up this sweet liquid, so agreeably made available to the ants—for their own jaws are useless for sap-extraction—to waiting for the actual voiding is only a simple step enough, and the stroking of the "cows" to speed up the appearance of the drop is another. The ants' invention of milking other insects is certainly no greater, as an evolutionary advance, than man's invention of milking other mammals.

Just as man's agriculture, whenever it becomes at all systematic, is extremely deleterious to most other organisms, what with the felling of forests, the draining of marshes, the killing of beasts of prey, the banishment of so many birds which need cover or solitude; so the dairying propensities of the ants constitute one of the most harmful of all their activities. So numerous are the species engaged in the protection

and often in the active dissemination of sap-sucking insects that a heavy toll is laid on plants, and man's efforts to keep his crops, flowers, and fruit-trees clean of these vitality-sapping pests are, in large part, rendered vain.

HONEY-POT ANTS.

Just as the harvester ants must store the seeds on which they live to tide over the dry season, so, too, the honey-dew eaters of arid regions must find some method of storage. Liquid food, however, is not easy to keep. The honey-bee has solved the problem; but the honeycomb is the climax of a long and gradual evolution. The ants never adopted this type of storage method, and the sudden invention of a pot or bin with an air-tight lid is not simple when evolution is working mainly by instinct. The honey-ants have arrived at a different solution, which is unexpected to us, but natural enough in insects—they convert some of the workers themselves into storage vessels. These living honey-pots have an enormously distensible crop, and the foraging-workers in the season of plenty feed and feed them by regurgitation until their abdomen becomes swollen to a huge spherical bag, the plates of its skeleton eventually becoming isolated on a great area of tight-stretched elastic skin. The "repletes," as they are called, are quite incapable of walking, and remain suspended by their claws from the roof of special chambers, in which a number of these "animated demijohns" hang side by side for months. In the dry season the ordinary workers stimulate them to regurgitate in the usual way, by stroking their heads, and so the whole colony is kept alive out of their capacious bellies.

This adaptation has been evolved independently in three sub-families of ants, always in desert countries. It is interesting to find that the single genus *Pheidole*

contains species adapted wholly to harvesting and others wholly to this storing of honey-dew. It is not known whether the repletes are predetermined for their task by the possession of specially distensible crops. More probably the possibility is open to all workers, but only a certain proportion of them have repletion thrust upon them.

THE LEGIONARY ANTS.

The predatory habit has been carried to its farthest extreme by the Legionary or Driver ants, already mentioned. These dreaded creatures, with their destructive instincts, their nomadic habits, and the vast numbers of their hordes, remind us of the invading hosts of Huns or Tartars in our own history. But here again the fundamental differences between man and insect appear. The most restless of the Mongols was capable of settling down to a stable and civilized life. But the Driver ants are for ever limited to their way of life by the iron hand of heredity. Their nomadism and their ferocity are permanent; their wanderings are barbarous invasions that never end.

Their blindness makes them more uncanny to us; but it is only one more instance of the subordination of sight to smell among ants in general. They usually exhibit great polymorphism among their neuters, the powerful soldiers attacking the largest prey—even horses and cattle are attacked and killed, when tethered—and rendering it available to the others; the small workers are equally ferocious and see to it that smaller creatures do not escape. The males, as usual, are winged; but the queens are permanently wingless, and grow into great egg-laying machines only excelled in bloatedness by queen termites.

CHAPTER VII

WARFARE AND SLAVERY

ANTS are among the very few organisms other than man which go to war. Individual insects or spiders, fish or birds or mammals, fight each other for food or mates or breeding-sites; but this is not war. When a herd of wolves attacks a herd of wild horses, and the prey vigorously defends itself, this is a first approximation to war. But strictly the term should be confined to battles between armies of the same or closely related species. In ants there are all gradations from the pure predatism of such forms as the Legionaries, against which no other ant defends itself, up through stages where the species preyed upon occasionally defends itself vigorously or even takes the offensive, to those of habitual warfare between closely allied species, and, finally, battles between different nests of the same species.

The best-known military activities of ants are those concerned with the raids of the slave-makers on the nests of the related species from which they wish to steal pupæ to be reared as slaves. The general biology of slave-making will be considered later; but the purely military aspects may be treated here.

In more peaceful species solitary workers scout about for food, and, after it is found, their return to the nest is followed by a large exodus of other workers to exploit the provisions. Similarly, the slave-makers' scouts go out in search of suitable nests to attack; and, when they return successful, all the neuters of the nest advance to the attack in a body. The Amazon slave-maker, *Polyergus*, forms in dense columns when near the objective, apparently searching for the scent. Such columns may be fifteen feet long,

with breadth up to six inches, and the march may last an hour, at an average speed of a yard a minute, or more. The leading ants are apparently sniffing eagerly for the scent of the slave-species. When this is found they dash forward to the attack. Some slave-species fly at once. Others offer violent resistance; but they are usually driven to fleeing with as many larvæ and pupæ as they can save, and to pursuing the Amazons, when they retreat, in the attempt to retrieve some of their booty. The returning column of slave-makers, guided solely by smell, follows the precise route which it took on the outward journey.

Forel has seen a whole army of Amazons lose its way and fail to find its objective; when the way is very long they may, though headed correctly, turn back again, apparently as the result of fatigue. There seems to be no leadership in the human sense, but some ants often appear to be very half-hearted and need to be tapped with the antennæ of more actively inclined animals before they will advance. Halts are often made to let the column close up, and usually again when the van has arrived close to the objective.

The same nest may be attacked day after day until there is nothing left to steal, or the inmates move to a new site. One Amazon colony, watched every day for a month, was seen to send out forty-four raiding expeditions, of which twenty-eight were complete triumphs, nine gained a few pupæ, and seven were total failures.

In one case observed by Forel some of the colony of *Formica fusca* which was attacked defended the nest with great vigour, while others succeeded in carrying the great majority of the brood out of danger, upon which the Amazons gave up the attack and began retreating. The *fusca*, however, violently excited, poured after and pursued them, and were so successful in harassing them that the enemy released the slave-young they had captured, and got away by utilizing

their superior speed. Such a defeat is exceptional. In this case it seems to have resulted from the front of the attacking column having come within sight of the defenders before they expected, and to the pause which then ensued while the rear was brought up being utilized by the *fusca* to man the nest thoroughly for defence.

Forel has also observed the attacked ants follow the slave-makers to their own nest, and launch themselves in hundreds in a vain assault upon it. The hostility of slave-making and slave-species is but a special case of normal prey defending itself. But different species of slave-makers are violently hostile to each other, and when they meet may wage battles as bloody as those against the slave-species. Finally comes the warfare in which the ants rival man, in which all the combatants are members of the same species. The Harvester ants seem to be the chief of such fighters, the accumulation of portable possessions leading, as with us, to cupidity and war. Such wars are fully as savage as those between the slave-makers and their victims, and may be very prolonged. One campaign between two neighbouring nests, described by Moggridge, lasted forty-six days; another, observed by McCook, which took place in Penn Square, in Philadelphia, lasted nearly three weeks.

One of the commonest causes of war is the building of a new nest too close to an old-established one, the ants in them displaying a territorial instinct very like that of many birds; on other occasions, however, scarcity of food may lead to hostilities between two nests previously at peace with each other.

The fact that two species of ants constantly nest in close proximity is the first step towards the form of parasitism which has had the name of slave-making applied to it, for, as Wheeler remarks, "different ant colonies, even of the same species, are so hostile that their mere existence in such contiguity implies that

one of the species is to some extent exploiting the other."

Some small ants live like brigands in dwellings close to the pathways of other ants, and snatch food from the returning workers, just as the skua compels the gull to disgorge its booty. The reason they are not attacked by their victims is not clear, but, as with the gulls and skuas, may lie in a difference in the disposition of the two species. Others, always of minute size, are permanent thieves. They make nests in the very walls of large ant or termite nests, and connect the galleries of the two dwellings by passages large enough for their own use, but far too small for their large neighbours to pay a return visit. An extreme adaptation to such a life is shown by *Carebara*, which steals from termites. The workers, in accordance with their mode of life, are among the smallest of all ants, while the males and queens are of more or less normal ant-size, and weigh over a thousand times as much. When the queen flies out on her marriage flight she takes a number of the little workers with her, clinging on by their jaws to the hairs of her legs. It has been plausibly suggested that this is an adaptation to the huge disproportion in size between the queen and the worker, since the queen could no more feed her pigmy offspring by regurgitation than could the ladies of *Brobdingnag* have successfully given the breast to a normal-sized human baby, and needs neuter nurses from the first. As an example of the blind nature of ant behaviour, it may be mentioned that workers, at the moment of the nuptial exodus, attach themselves indiscriminately to males as well as to queens, in spite of the fact that all which happen to take the male conveyances must die without fulfilling any useful function.

Occasionally weak, small ants live near the nests of large ones, merely, it would seem, to enjoy some protection from their powerful neighbours' proximity; and, at its highest, this relationship passes the low barrier

which separates one-sided exploitation from mutual service, and assumes, on the instinctive level, the form of a true alliance. For instance, in tropical South America a large brown *Camponotus* and a small dark-coloured *Crematogaster* jointly inhabit a curious arboreal nest which consists of a tunnelled ball of earth built round a tree-branch. (Such tree-nests of earth are usually overgrown with a fine "garden" of epiphytic plants, but these appear to owe their presence merely to accident, and to play no part in relation to the life of the ants.) The small-statured ant-people inhabits the outer layers of the nest, and its neuters rush out in defence whenever the nest is disturbed. The larger species lives in the centre, and, though extremely formidable, only emerges if the danger is serious. There is thus a division of labour between the two species analogous to that which obtains between workers or small skirmishing soldiers and large, heavy-armed soldiers of one and the same species. Even in this case, however, the young of the two species are kept and tended separately, although the adults continue to utilize the military advantages of the alliance by foraging together.

What is, in one sense, a further step has been taken by certain small ants such as *Leptothorax*, which, like many human parasites, get their living by making themselves agreeable. They make their galleries in the walls of *Myrmica* nests, but obtain their food directly from the *Myrmica* workers. This they do by creeping up on to their hosts' backs and licking away at their bodies and especially their mouth-parts. This titillation seems to please the *Myrmicas*, for they respond by regurgitating food for their little menials. These *Leptothorax* are thus in precisely the same boat as many of the beetles and other creatures which ants welcome in their nests, obtaining board, lodging, and tolerance in return for services rendered (Chapter VIII.). Their interest in the present connection comes from the

fact that, though in normal conditions they keep their own young stuck apart in chambers built by themselves, they can be induced, by being kept in artificial nests without any earth, to allow the *Myrmicas* to mix the broods of the two species. It is also interesting, as an example of ant plasticity, to find that, if they are kept by themselves in an artificial nest, they will after a time take to eating honey, insects, and other usual articles of diet, in spite of the fact that normally they take nothing but the product of the *Myrmicas*' social stomachs.

True slave-making has been evolved separately in the Formicine and Myrmicine ants. It was first observed by the younger Huber over a century ago, in the red slave-maker *Formica sanguinea*. The full biological meaning of its habit of raiding the nests of its black congener, *F. fusca*, for slaves, however, was not appreciated till nearly a hundred years later, when Wheeler found the clue to it in the habits of the queen. She is less independent than most other ant-queens, in that she is unable to found a colony by herself. After a successfully consummated marriage-flight she may either make her way into an established nest of her own species, or else into one of *F. fusca*. In the latter event, she collects a pile of pupæ, and kills any of the workers that attempt to take their possessions back. By the time the adult *fusca* workers hatch out, the robber queen must have acquired the proper smell, for they are wholly friendly, feed her, and tend the larvæ which hatch from the eggs she lays.

When adult *sanguinea* later emerge from the queen's own eggs, a mixed colony results. In different geographical sub-species of *F. sanguinea* different grades of slave-making propensity exist. In one the workers have none of it, and the mixed colony turns into a pure *sanguinea* with the death of the black workers kidnapped by the queen. In most, however, the *sanguinea* workers make periodic forays on nests of pure *fusca*, bringing

back stores of worker larvæ and pupæ. This habit is given up by some races when the colony has reached a certain size; but, finally, in still others is permanently continued. The black workers in the mixed nests are not slaves in the ordinary human sense, since they do not perform more menial functions or in any way occupy a lower position in the social scale than the red workers; they are rather like captives given complete equality with their captors, but forced to change their nationality.

The fact that some queens, like her of *Formica sanguinea*, are unable to store in their bodies enough food to feed their first batch of young is the first step towards slave-making. In one remarkable case—*Bothriomyrmex*, temporarily parasitic on *Tapinoma*—the foreign queen approaches the host nest, and is then forcibly seized by the workers. Once in the nest, the workers often attack her, but she then leaps up on to the back of one of the pupæ or, often, of the host queen, who is a good deal larger than she. Apparently, in those positions her foreign smell is masked by the local odour of patriotism, for she is then perfectly safe, just as on another plane of behaviour a spy may be safe in a foreign country if he masks his real feelings by assumed devotion to the local institutions. She spends more and more time on the back of the host queen, slowly but surely accomplishing her task of sawing her head off. By the time this is achieved, she has herself acquired the nest-smell, and is adopted, with the usual result that the *Tapinoma* workers rear up a brood of aliens, and the colony is eventually converted from pure *Tapinoma* to pure *Bothriomyrmex*.

Polyergus is allied to *Formica*; it also enslaves *Formica fusca*, but begins where the red slave-maker leaves off. The young queen here invariably invades some small colony of *fusca*, kills the queen by piercing her head with her mandibles—definitely adapted to such pugnacious acts by their pointed strength—and is

then adopted by the workers. The *Polyergus* workers are equally brutal in their raiding methods. The raids—always, for some mysterious reason, executed after midday—are highly organized, and any resistance on the part of the workers in the *fusca* nest merely results in the Amazons—as Huber christened the *Polyergus*—killing them with one nip of their sabre-jaws. Usually the *fusca* adults, whether as the result of instinct or experience, turn tail and leave their brood to the mercies of the hostile army. There is, in this case, a much greater division of labour between the captives and their captors, and the former more nearly merit the name of slaves. *Polyergus*' jaws are of purely war-like function, of no use in digging or capturing prey; they are a military aristocracy and do nothing but go raiding, while the *fusca* stay behind and do all the work of making the nest, obtaining food, and tending their captors' young. The masters have gone so far on the way to parasitism that they cannot feed themselves. Huber shut up thirty of them with some of their own young and plenty of food, but no slaves. Some actually died of hunger, and none even attempted to eat. A solitary slave was then put in. She at once fed the others, tended the larvæ, and began building operations. Another observer put a pile of sugar near a nest. Soon a number of slaves were gorging away at it. Some of the *Polyergus* then came out and pulled at the legs of the slaves. This was apparently a reminder of their duty, for they at once began to regurgitate their masters.

When the colony migrates, it is the slave-workers which carry their captors to the new nest, while in the *F. sanguinea* it is the slaves which are transported by the masters.

Finally come the ants which have reached the last stage of parasitism, and with it have lost the power of producing workers. The best known is *Anergates*, parasitic on *Tetramorium*, but the step has been taken

independently four or five times. The queen of *Anergates*, as in all these permanent parasites, secures her adoption by the host-workers by some unknown means; and then becomes swollen with eggs. The workers later, for reasons again unknown, murder their own queen. They tend the offspring of the usurper, all of which turn either into queens or males. The males afford a good example of what is known as neoteny, or reproduction while the body as a whole is still in an immature condition, since the general characters of the pupa-stage, including winglessness, are carried over into the adult phase. Mating must then take place within the nest, and is always between brother and sister; after mating, the winged queens fly out to seek new *Tetramorium* thrones.

It is interesting that most of the parasitic species of ants, and all those workerless permanent parasites, are scarce and very local; it is also interesting that the host is in every case closely related to the exploiter—this latter fact being explicable through the necessity for the workers to have nursing instincts adapted to the needs of the parasites' larvæ and pupæ.

CHAPTER VIII

GUESTS AND PARASITES

IN one strange respect the social insects, notably the ants and the termites, have attained a specialization not reached by man; and that is in the number of animals of other sorts which live in their communities, and are so closely adapted to such life that they can exist nowhere else. It is, of course, true that in or

about the habitation of man there are to be found plenty of animals of other kinds—physical parasites like flea and bug; economic parasites like rat, mouse, and cockroach; commensals like the cricket on the hearth or the house-martin; animals domesticated for food or draught, like hens, pigs, or horses; domestic companions and guards like the watch-dog; and pets like lap-dogs or parrots or goldfish. But the state of affairs is very different in the ants' nest. Their domesticated aphids and scale-insects we have already considered. There are no other kinds of domesticated animals, and no ant-pets deliberately taken into captivity because of their attractiveness. The same difference between insect and man, which has so often cropped up, is at work here again. Most of these "ant-guests" have been adapted to their mode of existence by natural selection, and their whole structure and instincts have been hereditarily modified. As we shall see, the tastes and aversions of the ants have doubtless contributed to the moulding of the guests' germ-plasm, but this moulding has been indirect, and there exists among the ants nothing similar to our conscious artificial selection, when we purposely breed only from those specimens of our pets or domestic animals which best please us, nor to an organized campaign against parasites or pests, like the ridding of Scotland of wolves or the Panama Canal zone from mosquitoes.

Finally, most of the aliens are of a size comparable to the ants themselves. If we imagined that in England our houses were, against our wills, inhabited by cockroaches as big as wolves and house-flies like hens; and that there were crickets to whose presence we were indifferent, although they were the size of our own children; and also pet-like creatures whom we liked because they rendered us some agreeable service, as it might be parrots which had the instinct of scratching our backs for us, or giant cats which we

allowed to eat our babies in their cots because they secreted hot rum-punch or some equally fascinating liquid; and that in France, say, and the United States there were similar sets of animals, willy-nilly sharing men's houses and reproducing there, only all belonging to different species from those in England; and, finally, that they were all incapable of existing permanently anywhere outside our houses; then we should begin to get some idea of the menagerie of guest-animals in the habitations of ants.

The evolutionary method which a great many of these creatures, and probably that numerous host to which the ants show active friendliness, have adopted is to exploit their hosts' peculiar form of greed, which, in turn, has been specialized as a consequence of their trophallaxis. They have developed glands producing secretions similar to those exuded by the ant-larvæ themselves, and in return for the privilege of licking up these tasty juices the workers will feed them just as they feed the larvæ. Sometimes the secretions of the guests must be possessed of new and overpoweringly attractive properties to the taste, so that the nurses even neglect their proper charges in favour of these aliens. We know, alas! of human parents who will neglect their children for drink, but this is as if a mother were to abandon her baby for the charms of gin exuded from the body of a changeling.

Wheeler admirably sums up the situation as follows: "Any insect possessed of these glandular attractions . . . can induce the ants to adopt, feed, and care for it, and thus become a member of the colony, just as an attractive and well-behaved foreigner can secure naturalization and nourishment in any human community. But the procedure among the ants is more striking because the foreigners are so very foreign. . . . Were we to behave in an analogous manner we should live in a truly Alice-in-Wonderland society. We should delight in keeping Porcupines,

Alligators, Lobsters, etc., in our homes, insist on their sitting down to table with us, and (in some cases) feed them so solicitously that our children would either perish of neglect or grow up as hopeless rachitics."

Perhaps the strangest of these alien exploiters are the Staphylinid beetles, *Lomechusa* and its relatives. The habits of *Lomechusa* were brought to light by the Jesuit entomologist Wasmann. It lives exclusively in the colonies of the red slave-maker, *Formica sanguinea*. The adult beetle solicits food from the ant-workers by stroking them with its antennæ; its abdomen is covered with bunches of golden hairs, called trichomes, which surround the opening of special glands and act in lieu of teats for their secretions; the beetles present them to the ants, working their abdomen forward over their back; and the ants eagerly suck off the oily secretion, rewarding the beetles with regurgitated food. The grub-like larvæ apparently exude fatty secretions of much price, for not only are they fed with regurgitated food by the worker-ants, not only are they tended and moved about with the ants' own brood, but are allowed to eat the ant-larvæ. Indeed, the ants appear to prefer the *Lomechusa* grubs to their own, with the result that a large part of the brood dies.

It is in colonies heavily infected with *Lomechusa* that pseudogynes (p. 22) are produced. It has been supposed that the ants eventually realize the shortage of workers and attempt to convert queen larvæ into workers by altering their diet—but too late to have effect. Another possible explanation is that the queen larvæ, being neglected, fail to get the right food and are therefore switched over towards the worker type of development. These pseudogynes, which usually comprise five per cent. and may reach twenty per cent. of the population of an infected nest, are described as "lazy, cowardly, and incompetent." When a nest is

heavily infected it can produce no queens, and will soon die out.

It might be thought that the whole race of red slave-makers would be on the road to rapid extinction owing to the beetles. But, as a matter of fact, the species is abundant and prolific, the parasites' infection only local and sporadic; and this is true, not only of this host and this parasite, but of all other deleterious ant parasites and their hosts, whether the parasites be insects of other groups or ants of slave-making or parasitic habits. The greatest danger to a deleterious parasite is to be too effective in inflicting harm upon its host. For if the host decays, it decays too; if the host is extinguished, it, too, becomes extinct. In general, it is the very widespread successful or plastic species that supports the greatest number of kinds of parasites, because they are less likely to succumb under the burden. The extraordinary abundance of gall-producing insects that affect the oak is an example from another group. In addition, if the parasite is not to kill itself by killing its host, its numbers must be kept down, either by the host's acquiring partial immunity or by great difficulties of dispersal from host to host, or by some other means. Thus, as a general law of parasite existence, the parasite must be less numerous or in some other way less biologically dominant than its host.

The check on *Lomechusa* is a very curious one. The ants treat the beetle-grubs as they do their own brood. This ant buries its full-fed larvæ in the soil; here they spin cocoons, and are then, as pupæ, dug up again, cleaned, and piled in special chambers. Now, the *Lomechusa* larvæ, though they, too, must be buried to pupate, spin no cocoons, and infallibly die if dug up again; so only those few buried beetle-pupæ which the ants fail to unearth succeed in turning into adults, and the population of *Lomechusa* is thus regulated down to sufficiently low proportions.

The closely-related beetles *Atemeles* and *Xenodusa* are interesting in that they have two hosts: in the summer they live in *Formica* nests, but take up their winter quarters with species of *Camponotus*, the carpenter ant. They only breed, however, in the summer, so that the *Camponotus* does not have its brood affected, and produces no pseudogynes.

Several hundred species of befriended guest-beetles are known from ants' nests. All of them possess the special glands and their teat-like trichomes. Curiously enough, the hairs of the trichomes are almost always yellow, and the general colour of the beetles an oily red. In addition, their jaws are often highly specialized to feed on the liquid pumped up by the ants, and their antennæ modified to imitate the soliciting action of the antennæ of other ants. The addiction of the ants to the liquors and rich buttery sweetmeats which these produce is revealed in the way in which, at the threat of danger, they seize the beetles and carry them to safety.

Other kinds of insects also exploit the ants' greed. During the last decade, for instance, it has been discovered that, of all unlikely creatures, some of the lovely blue butterflies (*Lycænida*) are, at one stage of their development, ant-devourers. The caterpillar lives the usual vegetarian caterpillar life until it is half grown. It then descends from its food-plant and stations itself in an ant-track. It appears to produce desirable secretions, for the ants, on finding it, carry it off to the nest, where it lives at the expense of the community, giving only luxuries in return for necessities, until it is time for it to pupate.

Other ant-guests, not being ambulatory bars or confectioners' shops, are treated with hostility by the ants, and must gain their living by stealing and escape destruction by agility or strong defence. For instance, *Lepismima*, a primitive wingless insect of the silver-fish type, steals impudently from *Lasius*. Janet has described

the scene when the worker *Lasius* bring back food to the nest. The *Lepisminas* at once begin to show by their excited movements that they smell something. The returning workers meanwhile begin to regurgitate food to their stay-at-home sisters. As the food is being transferred, feeder and fed face each other, with the fore-parts of the body raised. A thief approaches such a couple, crawls below their heads, suddenly snaps up at the liquid as it passes from mouth to mouth, and rushes off. The ants, being in rather a delicate pose, are usually not able to turn in pursuit before the *Lepismina* is out of reach; and, in any case, it is covered all over with smooth scales, which render it hard to catch.

Another thief-guest relies on mechanical protection. It is compassed all round with a series of long scales, somewhat in the shape of the long caparisons worn by mediæval horses in the tourney; some of these scales can also be thrown forwards to form a more or less tubular protection for the proboscis. In addition, there are still bristles which protrude straight out from its flanks. It, too, steals from the workers as one is feeding another, reaching up with its protected mouth. If an ant tries to get under its defences, the bristles act like cats' whiskers to give notice of the attack, and the scales on that side come down flat on to the ground, conferring upon the attacked side of the animal the properties of a tank.

Then there are parasites—thieves, if you will—of which the ants take no notice. Wheeler has described the larva of a little fly (*Metopina*) which exploits an ant of the genus *Pachycondyla*. The fly-grub clings like a collar round the neck of the ant-grub; the latter is fed by having pieces of insects placed in a natural trough on its ventral side; and on this happening the *Metopina* uncoils and reaches out for a share. Apparently it acquires the smell of its host, for the ants do not notice it at all, and clean it with the rest of the

ant-grub. Its adaptation to safe emergence deserves mention. Its development is adjusted to that of its host-grub, and when the ant-larva pupates, the fly-larva, which is, of course, enclosed in its host's cocoon, moves to the hind end and there pupates also, forming a puparium very much flattened against the cocoon wall. When the callow adult ant is ready to emerge, the workers bite open the front end of the cocoon and pull it carefully out, and the apparently empty cocoon is then taken off and thrown on the refuse-dump. The fly's pupal period has been adapted by natural selection to be longer than the ant's; thus when the fly emerges, it finds no obstacle to a safe exit. Here, again, the parasite merely takes toll from the ants' excess; there is no sign of its inflicting any damage on the individual larva it steals from, or on the colony as a whole.

The most extraordinary of tolerated guests is perhaps the externally parasitic mite *Antennophorus*, some of which infest those same *Lasius* which we recorded as being almost blind and keeping white ant-cows underground. The mites are quite large in comparison with their hosts, much like a cat or a smallish monkey in relation to a man, and up to four (or rarely six) may be found on one ant. They behave in a remarkable way as regards the positions they take up, always placing themselves so that the ant's balance is not upset. When there is one, it is always under the chin; if a second comes, the two move to the two sides of the abdomen; a third will occupy the place under the head; a fourth will occupy one side of the head, while the third will move to the other; a fifth will once more attach itself below the chin; and the rare sixth will occupy the only vacant space on the top of the abdomen.

The ones attached to the head feed on regurgitated drops as they pass directly between the mouths of their own *St. Christopher* and another ant; or they

cause it to "cough up" for their sole benefit by stroking it with their fore-legs, which are moulded into a passable semblance of ants' antennæ. Those mites which ride on their host's abdomen stroke other ants, or snatch at drops passing between other worker-pairs.

The strange fact is that the mites appear not to produce any secretion in exchange; and the ants try to throw off their riders when they are mounting, though afterwards they tolerate them once they have settled into their positions of equilibrium. One can only conjecture that the mites have the nest-smell, that once in position they are not much of an annoyance, and that their soft strokings are like enough to the solicitations of other workers to delude their hosts. Wheeler suggests that the blind ants feel towards them as we might to pleasant pets; this *may*, of course, be so, but seems on general grounds rather unlikely.

These instances constitute but a sample. Already more than 2,000 separate species of ant-guests are known, somewhere about half the number of known species of ants; and these include representatives of mites, spiders, crustacea, and most of the orders of insects—indeed an amazing menagerie! "Where the feast is, there shall the vultures be gathered together"; and the very success of ants has led to their being exploited by these hordes of other creatures.

CHAPTER IX

TERMITES OR "WHITE ANTS"

We cannot exclude termites from our survey. For though actually quite unrelated to true ants, they are so like them in many ways as to have earned the name of "White Ants." The organization of their colonies is very like that of ants' nests, and yet sufficiently different to afford much food for reflection. In many ways they excel even the ants in strangeness of habits and social organization; but for all their abundance and their marvels of structure and instincts they have not attained the same supremacy in the biological world. They still bear the marks of their origin from an altogether lowlier stock of insects; hardly any of them can tolerate daylight, and they have not been very successful in pushing far out of the tropics.

They belong to the Isoptera, one of those primitive insect orders which have no true metamorphosis, but hatch from the egg in a form essentially like the adult. Almost all of them are tropical or sub-tropical. A few penetrate to higher latitudes; but in striking contrast to the ants, there are not more than forty species or so in the United States, and only two of them reach the parallel of Boston. Not only this, but whereas the highest sub-families of ants are the most successful in invading cool climates, the highest family of Termites, the *Metatermitidæ*, is almost exclusively tropical.

They may be divided very conveniently into four families, arranged in a single scale of progressive specialization. One of these, the *Mastotermitidæ*, comprises but one living species confined to Australia, though fossils show that in the early tertiary epoch the

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family was widely spread in Europe, and probably elsewhere. Thus *Mastotermes* has the same sort of relation to higher Termites, both in structure and distribution, that the duckbill *Platypus* has to the remainder of living mammals; and just as the *Platypus* betrays the relationship of mammals to certain reptiles, so *Mastotermes* shows that Termites are sprung from Orthopteran ancestors, since it betrays close affinities to a family of cockroaches, the *Protoblattidæ*, which died out in the Permian period.

All Termites are fully social, with neuters doing the work of the colony. But there are two, and probably three, fundamental distinctions between their social organization and that of ants, bees, and wasps. In the first place, the colony is always started by a "royal pair," a queen together with the male who has fecundated her, instead of by a solitary queen. Secondly, the workers, and other neuter castes when present, are of both sexes in equal numbers, instead of all being sexually-arrested females. And, thirdly, it is probable that the various main castes at least are all determined by heredity, and not by means of differences in diet. Thus the sexes are of equal social importance instead of the males having a purely reproductive function; and, if the third point be established, the social organization is in a sense on a lower level than that of ants or bees, since the determination of the various castes depends wholly on a germinal mechanism, and not at all on the instincts of the nurses.

There exists a complete gradation from colonies with only a few score individuals, and only one type of neuter caste, up to communities which pass the million mark, outdoing even the ants in numbers, and exhibit an extraordinary polymorphism. In the most developed communities there exist the following types: (A) *Reproductive caste*.—(1) First form reproductives ("queens" and "kings"); (2) second form

reproductives, or substitute queens and kings; (3) third form reproductives, or worker-like substitute queens and kings. (B) *Worker caste*.—(4) Workers, male and female. (C) *Defence caste*.—Either (5a) soldiers or else (5b) peculiar snouted defence forms called the *nasuti* or “nosy ones,” these also both male and female. This makes ten castes, five male and five female. In addition, both the workers and the soldiers may be differentiated into sub-castes, differing just as in ants in size and proportions of heads and body, bringing the total numbers of distinguishable forms up to twelve or fourteen.

In almost all Termites the true king and queen alone among the castes are fully pigmented and capable of facing the light of day. They are winged, but, like the queen ant, break off their wings on descending to earth, after leaving the nest on their one flight. This flight is not a true nuptial flight, but a dispersal flight, since mating takes place, not in the air, but after they have descended (in couples) to the ground, and shed their wings. Later, the queens grow to an incredible size, flabby white sausages over four inches long, and proceed to lay an egg about every two or three seconds for the remainder of their natural life.

The second form reproductives have all the characteristic organs of the reproductives, but reduced in size or quantity, less pigment, smaller brain, eyes and reproductive organs, and rudimentary wings; while the third form reproductives carry the loss a step further, and have no wings, scarcely a trace of pigment, rudimentary eyes and further reduced brain and gonads. These two castes, of substitute queens and kings, are what we have called neotenic (p. 55); they carry over the more primitive characters of the later or earlier larval stages into the adult reproductive phase; their origin would be accounted for on the hypothesis that all processes of differentiation, save the one concerned with ripening the gametes, were slowed down during their

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development. Their function in the colony is somewhat obscure. They are usually believed to be reserve reproductive units, ready to take the place of the true kings or queens should they die; but this is not certain, nor whether they, as well as the full kings and queens, normally exercise their mating instincts. In the colonies of some species the true queen never develops, but her place is taken by a harem of second form females, sometimes over a hundred in number.

The workers are white and pigmentless, lack wings, and their eyes are rudimentary or absent; like the independently evolved worker-caste of ants, they are chiefly concerned with nest-building, food-seeking, and food-distribution, and the toilet of the other castes; but unlike worker-ants, they have brains smaller than the reproductives. The soldiers are wingless, with huge heads and jaws, and usually use them in the defence of the colony. They have some hardened and pigmented skin, but only on the head; and thus they are like the goblins in McDonald's "Curdie and the Goblins," cast-iron in the head but soft and defenceless elsewhere. Since they, too, are permanently subterranean, their eyes are degenerate. The *nasuti* also defend the colony, but in a way which has the same sort of relation to the brute strength method of the soldiers as has chemical warfare to bayonet fighting. Their jaws are minute, but in return the frontal gland which most termites possess is in them much enlarged, placed conveniently forward at the tip of the snout, and made to secrete an adhesive liquid which certainly can immobilize the enemies by sticking their limbs and antennæ together, and perhaps has poisonous properties as well.

In some forms the secretion of the *nasuti* appears to be used to dissolve hard substances which are in the way of the workers when building; it is stated that even concrete may be eroded in this way!

Miss Thompson has discovered that the young

reproductive forms can be distinguished from the worker or soldier at hatching, and probably the worker from the soldier also, by differences in the size of brain and eyes. This would make it practically certain that at least the three main castes were predetermined at the moment of fertilization, just as are the sexes in most animals, or the different forms of flowers in Primrose or Loosestrife. The sub-castes or workers and soldiers, however, are presumably determined, as in ants, by differences in the amount of food secured by the growing young combined with differential powers of growth in different parts of the body. The origin of the subsidiary royal forms is unknown.

How the genetic machinery works we have at present not an inkling. It has been further asserted that while the first form royalties can reproduce all the castes, the second form reproductives cannot give rise to the first form, and the third form neither to the first nor to the second form. The mechanism underlying this is equally obscure, though it, too, might be genetic in nature, the two substitute forms being recessive.

The food economics of the termitary outdo those of the ants in strangeness. To start with, the higher, wood-eating termites are unable to digest their food unaided; they have to rely on certain parasites turned helpers. These symbiotic inhabitants of their gut are ciliates called Trichonymphids, large for single-celled animals, with bizarre movements and a very peculiar arrangement of their cilia. They are normally only found in the interiors of the adult workers and soldiers, not in the young, nor in the reproductives.

Now, in higher termites, the whole termitary derives its existence almost entirely from wood, and other dead plant tissues which consist either of cellulose or the modified woody cellulose, lignin. Neither cellulose nor lignin, however, are attacked by the digestive juice of any animal higher than snails. The

Tryphonymphids, on the other hand, produce cellulose-splitting ferments; they thus supply their hosts' deficiencies. The termites supply the food for both partners; the protozoa chemically chop it up until it is soluble, and both live on the products of their joint activity. The reason why Trichonymphids only live in the workers and soldiers is doubtless that these alone eat raw cellulose, the other castes being supplied by them with liquid products of digestion.

Experiment has proved what observation suggested—the indispensability of the Tryphonymphid for the termite. The protozoa cannot stand such pure oxygen; in an oxygen atmosphere all of them die in a few days, while the termites themselves are quite unaffected. Workers thus rendered protozoa-less die of starvation in a few weeks, although provided with all the wood their hearts could desire. They devour the wood with all their ordinary appetite, but nothing happens to it in their interiors, and it passes out unchanged, without their profiting from it in the slightest. If, however, they are artificially reinfected, they become capable of digesting their food once more.

The food, once digested in this way, begins a direct or indirect circulation through the colony, compared to which the ants' methods are primitive. This food circulation has been likened to the circulation of blood and lymph through our own bodies; and, though the comparison is but rough, yet it is exact in one fundamental respect—the food does constitute a nutritive stream, by which the various units of the whole are bound together in mutual dependence. First, as in ants, the termite workers regurgitate, but what they regurgitate is only partially digested. Secondly, they can dispense more fully digested food, but this must be done *per anum*, only part being absorbed in its passage through the intestine, and the rest passed out behind for others' consumption. Thirdly, some of the absorbed food is worked up in

the "salivary" glands into a liquid with nutritive and doubtless pleasing properties, and drops of this are secreted for others. It seems probable that the different castes exude different substances, and that, in the darkness of the nest, they are recognized by their taste. The full-grown first form queen appears to secrete the most delicious exudate of all, and is invariably seen to be surrounded by a regular court of workers, who, however, are not doing obeisance, nor even tending her, but licking up the royal juice as it exudes, sometimes with such gusto that they perforate the royal skin.

Just as in ants, this fondness of the termites for such rich food has led to their exploitation by a number of guest-insects who have mastered the secret of producing similar substances. Presumably in accordance with differences in the construction of termites' mouths from those of ants', their guests have not developed the teats of hairs characteristic of ant-guests, but instead have produced thin-walled, lickable structures, swollen bellies, or special protrusions of the body. In addition, a great many have acquired the physogastry or extreme swelled-belliness characteristic of the full-blown termite queen. This is usually produced by the enlargement of the fat body, but may be due to enlarged gut or gonads. With increase of abdomen, there generally goes decrease of head and eyes, thorax and wings. A curious fact about the guest-beetle *Spirachtha* is that it appears to hatch out in more or less beetle-guise, and only (like the termite queen) to acquire the swollen belly and lickable outgrowths later.

It would naturally be supposed that this swelling was directly concerned with the production of more fatty delicacy, and more surface off which it could be licked. However, it appears to be the fact that some of the insects which are never licked, but to which the termites are either indifferent or hostile, also

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acquire physogastry. It has been accordingly suggested that physogastry is in part due to some substance in the food acting like a hormone, and that selection has later stepped in to exaggerate and utilize the result.

There are no examples known of slave-making or workerless parasites among termites; in fact, the social insects most frequently nesting inside or near termitaries, and profiting by the shelter, protection, and food provided, are ants. A few termite species, however, are thieves, and some *Microtermes* steal fungus and prepared "soil" from the vegetable-gardening termites *Odontotermes* and with the spoils make gardens of their own.

The nests of termites are on the whole more interesting than those of ants. This is natural, since the termite is so intolerant of light and air that, unless it lives wholly under the level of the soil, it requires something more solid and permanent. If, as from one point of view we are justified in doing, we regard the termite colony as one individual, then the nests of higher termites are to be compared with the thick armour-plate of giant crabs or tortoises or some dinosaurs, or the shelly fortress of an oyster or a conch. But armour-plate, however successful an expedient for the time, in the evolutionary long run leads animals into a blind alley. The more efficient the dinosaur's armour, the less need of speed, brain, or acuteness of sense to avoid enemies; the more colossal and steely-sided the termitary, the less readily can its inhabitants change their abode, the less are they forced into a healthy give-and-take with the forces of Nature. Thus in the long run the termites have become a race of gnomes, stranger and more remote from the main stream of life than ants or bees, supreme within their own limited darkness, but in a sense aliens in the greater world.

The lower termites in general make nests not unlike those of ants, diffuse tunnellings below ground,

or in decaying logs and stumps. The higher types, on the other hand, build what have been styled concentrated nests, definite edifices sharply marked off from the rest of the environment. Perhaps the most striking are the giant earthen termitaries of the African grasslands, which, gradually built up over the original tiny subterranean chambers excavated by the royal founders, may reach a height of twenty feet and more, so strong in construction as to be almost indestructible with anything less powerful than dynamite. Very similar nests are to be found in Australia, too. In the hottest part of this latter continent some species construct long, thin, wedge-shaped buildings, which are called compass-nests owing to their always being aligned north and south; this arrangement doubtless is an adaptation to the great heat, since less surface is thus exposed to the midday sun. In Africa, strange stalked nests are found, with a mushroom top apparently serving as an *en tout cas* to protect both against sun and rain. Other nests from the rain-forests of the same continent bulge out like a cluster of sausages from the trunks of trees, and are protected from the rain by a whole series of inverted V's of cemented wood-pulp built on to the tree-trunk above them. While the ground-nests are usually built of earth, the material of the tree-nests is for the most part chewed and semi-digested wood cemented with saliva into a paper-like mass. Usually they are round or oval, and may reach the size of a respectable barrel. Termitaries, unlike ants' nests, never have any visible entrances. This is owing to the light-shunning of their inhabitants. The termites either burrow through the surrounding soil or wood, or, in many of the higher forms, though they travel on the surface of the soil, run up tunnels over their roadway as they advance.

These tunnels may be several score yards long, and by their aid the colonial organism extends its tentacles

in every direction. When a large termite colony by this means penetrates into a house, its ravages may for a long time remain unsuspected, since the workers will devote themselves to eating out the inside of every wooden object available. Eventually, they will reduce walls, floor-planks, tables, and chairs to a mere shell, and the householder is made aware of what has been going on by the collapse of his furniture or his house.

Owing to these habits, termites are much more destructive than ants. It is, of course, not only the woodwork of houses which they invisibly devour. Fences, railway-sleepers, telegraph poles, boats, landing-stages, bridges—all are grist to their mill. But it is not merely material civilization whose spread they retard. Paper, too, is made mainly of cellulose, and the addition of printer's ink unfortunately does not render it unpalatable to the termites. Thus some of their most serious ravages are committed on documents and books. Von Humboldt records that, when he was in the hotter part of South America he rarely saw any book over fifty years old, the rest having gone to feed termites. It has been suggested with a good deal of reason that this is one (though doubtless by no means the only) cause of the slow development of culture in the tropics; and it is certain that any tropical nation that wants a flourishing and enduring civilization will have to construct, what some have already made a beginning with, termite-proof foundations for its buildings, more particularly the buildings where its libraries and its archives are housed, and for any structure in which any degree of permanency is required.

On the credit side of the termites' account, however, must be entered the fact that, unlike ants, they are not only not deleterious but actually beneficial to agriculture. In temperate regions, as Darwin showed us, earthworms perform a very important task in preparing and renewing the soil for plants. Termites per-

form a very similar function in the tropics, but probably on a greater scale, and certainly with greater rapidity. Their tunnellings aid mechanically, their protozoa digestion chemically, in hastening the disintegration of those resistant substances, cellulose and wood; and in this way much of the capital of life, which would otherwise stay locked up for years in a strong-box of chemical unavailability, is by them rapidly brought back into circulation.

Strange to say, fungus-gardening has arisen in termites as well as in ants—a good example of independent evolution which may be taken to heart by some of the more radical diffusionists who maintain that in human culture nothing has ever originated more than once. The fungus-gardens may reach an even greater size and perfection than in the ants; the nests containing them are sometimes provided with chimney-like structures, which are probably ventilating shafts designed to help in the regulation of temperature and moisture. It has at any rate been shown that the diurnal rate of temperature in the nest is only 9° C., when that outside is over 20° C. The workers and soldiers keep to the more solid diet of cellulose, and leave the fungus to the reproductives and the young. The young use the gardens as a combination of pasture and nursery, and present a pretty enough picture as they browse—white miniature lambs against herbage of equal whiteness.

It can be prophesied of the termites in their armoured colonies, with even greater assurance than of the ants, that they have reached the end of their evolutionary tether, and will continue, as a group, with no essential change and no real progress. Holmgren, one of the authorities of the group, has pointed out that their evolution is accompanied first by that specialization of their societies which has already been mentioned, secondly by an enlargement of their brains, and thirdly by a degeneration of their bodies.

This is a fate which has often been prophesied for the human species. It remains to be seen whether the fact that man lives partly on the level of reason and foresight will enable him, through sport, physical exercise, and eugenics, to surmount the danger.

CHAPTER X

INSECTS AND MAN

So our brief review of the ants and termites comes to an end. We are now in a better position to judge of the fallacies into which so many writers on social insects have fallen, to some of which reference has been made in the introduction to this book.

A few have been guilty of gross over-simplification. Bethe, for example, wished to make of ants and bees the merest reflex machines, incapable of profiting by experience or recognizing the locality of their nests in any way at all similar to our recognition of familiar spots. Others, again, would have it that they were wholly colour-blind, which, if true, would have robbed the brilliant colouring of flowers of all biological meaning.

But the majority adopt a more popular and a more insidious view. They either turn insects into miniature human beings, or else ascribe to them wholly magical attributes. Bethe himself was obliged to postulate in bees a mysterious sense of direction which operated through none of the ordinary channels of sense; and the powers ascribed to instinct by writers such as Fabre would enter the realm of miracle—if they were

true. On the other hand, lay writers, like Maeterlinck in his book on *The Life of the Bee*, and still more that on *The White Ant*, ascribe all the achievements of insects to intelligence, and draw invidious comparisons between their minds and that of man. It would really seem that such writers have never heard of Darwin, or at least never read his works or even a modern summary of what is meant by Natural Selection; that they are ignorant of ordinary physiology, and unaware of the extreme complexity which wholly mechanical and non-conscious behaviour can reach in ourselves.

Maeterlinck, for instance, says that the termites are more intelligent than we are because they have found out how to digest wood, to dissolve concrete, and can mould the bodily form of their citizens at will, sterilizing them, turning them into born soldiers, or making them mere egg-laying machinery. But the termites can no more help having the wood-digesting protozoa in their gut than dogs can help having worms, and, since no one has ever thought of ascribing to human intelligence the existence of the admirable ferment trypsin in our pancreatic juice, or the fact that our eyes are constructed as very efficient cameras, there is not the slightest reason for doing so in the case of the termites' chemical achievements. In termites, too, there is every reason to suppose that all the castes are predetermined by heredity; if this were so, their "intelligence" in possessing royals, soldiers, and workers would be precisely on a par with the "intelligence" of human society in generating people who are fair-haired or dark-haired, tall or short, temperamentally athletic or intellectual.

Even where, as in ants and bees, the differences between neuter and queen are determined by feeding, the whole capacity for reacting to the two diets in these two different ways is given by heredity, as is also the instinct of the workers to feed the young in these par-

ticular ways—for they will do so without any training—and the only point left to be decided by intelligence is the relative numbers of queens and workers to be produced. As a matter of fact, we do not yet know anything as to how the right proportion of the castes is arrived at, and it may even be accomplished by some almost automatic response. In any case, the actual bodily shape of the different castes has been arrived at through the operation of natural selection, and is wholly different from the moulding of his domestic animals and plants achieved by man, as when the fancier breeds a new strain of fowls up to a standard previously laid down, or Sir Reginald Biffen deliberately sets about creating a new sort of wheat.

Finally, there is another fallacy which from time to time crops up. We are told that, as we elaborate our civilization, as we mechanize it by trusting to the achievements of applied science, as we specialize more and more in occupation, we are inevitably heading for a condition in which our society will come to resemble an enlarged ants' nest or gigantic termitary. For this prognostication, too, which has been recently advanced, among others, by Dean Inge, there is no shadow of biological support. Partly, it seems, this view is based upon conscious or unconscious Lamarckism; it is felt that, if we specialize, the structure and modes of thought of our offspring will gradually become fixed in the grooves of society's various specialisms. The modern study of heredity has luckily proved the baselessness of any such fear. For the rest, it is based on a particular theory as regards the course of evolution. All types or groups of animals and plants—say the upholders of this view—pass through a period of rapid evolutionary change to reach a later phase of stability. The first phase is characterized by great plasticity of the germ-plasm, while in the second it becomes fixed and resistant to change.

Now, in the first place, this idea of the plasticity or

fixity of the germ-plasm is pure hypothesis, proposed as a possible explanation of the undoubted fact that many types, after rapid initial evolution, do settle down later to a slowing or stoppage of progress. But it by no means follows that the cause of this resides in the germ-plasm; it may just as well depend on the animal having become so specialized that few or no changes which actually take place in the germ-plasm could be of any biological advantage. And, in the second place, the fact that rapid rise, followed by stability and finally by decline, has frequently occurred during evolution is no reason for erecting a universal law upon the body of the facts, any more than the frequent rise, stable maturity, and eventual decline of nations is any valid reason for supposing that such a cycle is a necessity for all nations.

It is always possible, in the past instances of such evolutionary cycles, to assign reasons for the slowing down of progress and the eventual decay or extinction of the group. The limits of physical specialization account for the one, and the rise of new groups from an initial stage a step higher than that of the earlier group, a rise frequently aided by cosmic accidents such as changes in climate or in the distribution of land and water, accounts for the second. If one specialization can be achieved without enslaving the body and turning it into a particular kind of tool-box, and progress, too, can take place by the aid of conscious methods, by improvement of tradition and social organization, and if necessary by deliberately controlled breeding, the whole case is altered, and the limitations fall to the ground like the walls of Jericho at the blast of the Israelites' trumpets. Man alone among animals has fully passed from the one condition to the other. It is curious that a writer who, like Dean Inge, has so acutely criticized the idea of inevitable progress should not have applied the same criticism to the idea of inevitable arrest of progress.

Be that as it may, the ants and the termites are still on the biological level on which, though mind has come to play a considerable part in individual and social behaviour, the evolution of the race is still entirely dominated by blind and automatic forces such as natural selection. Man, on the other hand, is on the level where evolutionary change can be brought about by changes in tradition and by conscious purpose, applied either to this tradition or to the germ-plasm of the race.

There is thus no reason to suppose that man is destined to sterilize nurses or manual workers, to breed armoured or gas-resistant soldiers, communal parents the size of whales, or an intelligentsia all head and no body. Nor is there any reason to suppose that he will settle down into a mechanized and stable condition of existence—at any rate, for the long millions of years where there will still be things for him to discover, still new enjoyments to taste, and still new changes to make by which the life of society and of the individual may be improved. By virtue of his nature, he knows that he can discover new truth, can create new works of art, can control his own destiny; and this is precisely what even the most intelligent ant or the most specialized termite entirely and for ever lacks.

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